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### Errata

- Page 63, line 16, for "*Portoviejo*" read "*Porto Velo, Prov. Oro.*"  
 Page 118, line 6, for "*Leptaemia*" read "*Leptotaenia*."  
 Page 143, line 20, for "*A. arnophyllus*" read "*A. argophyllus*."  
 Page 154, line 19, for "*A. unitensis*" read "*A. uintensis*."  
 Page 154, line 20, for "*Xylophacos unitensis*" read "*Xylophacos uintensis*."  
 Page 195, line 14, for "*Dupata*" read "*Dupatya*."  
 Page 222, line 6 from bottom, for "*var. bernardiha*" read "*var. bernardina*."  
 Page 229, line 17, for "*A. chamaeluceae panguicensis*" read "*A. Chamaeluce panguicensis*."  
 Page 234, line 14, for "*H. Newberryi*" read "*X. Newberryi*."  
 Page 241, line 21, for [volume] "*38:*" read "*32:*"

BULLETIN  
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## Studies on the flora of Northern South America—II\*

H. A. GLEASON

(WITH PLATE I)

THE STELLATE-TOMENTOSE SPECIES OF *CENTROPOGON*

The genus *Centropogon*, as represented in northern South America, may be readily divided into a few sections which are at once recognizable by certain very obvious characters. Among these a group of tomentose forms is especially noteworthy because of the characteristic branched hairs, a feature rarely found elsewhere in the genus. In most species, these hairs closely resemble the well-known hairs of *Verbascum Thapsus*; in others, by shortening of the axis and reduction in the number of branches, they are reduced to small stellate structures, and in a few species simple hairs may be found among the branched. These typical hairs are regularly found on the young stems, petioles, and peduncles, and usually as well on the hypanthium and perianth, although in many species they are soon deciduous, leaving parts of the plant essentially glabrous. The flowers are always axillary, the peduncles arising from the axils of the upper leaves; the hypanthium is broadly hemispheric, occasionally varying to short-cylindric; the corolla is brightly colored, except where the surface is concealed by the indument, with a conspicuous tube and strongly decurved, falcate lobes; the two lower anthers are bearded; the fruit is a berry.

The section is best represented in the mountains of Colombia and Ecuador, but extends from this center north into Central America, east into the Andes of Venezuela, and south into Bolivia. The species known to me may be distinguished by the following key.

\* Contributions from the New York Botanical Garden—No. 263  
[The Bulletin for December (51: 469-512) was issued 17 January 1925]

- A. Corolla tube stout and short, rarely twice as long as the lobes; anther-tube densely tomentose, long-exserted; sepals ample or foliaceous, exceeding the hypanthium, the sinuses narrow or acute.  
 Sepals ovate or ovate-lanceolate, serrate, broadest above the base.  
 Anther-tube covered with tawny hairs.  
 Anther-tube covered with purple hairs.  
 Sepals narrowly triangular, serrate or entire, tapering regularly from the base to the apex.  
 Corolla externally and lower leaf-surface thinly pubescent.  
 Corolla externally and lower leaf-surface densely stellate-tomentose.
- B. Corolla-tube slender and elongate, 2-5 times as long as the lobes; anther-tube pilose in the fissures to glabrous, the summit of the filaments little if any surpassing the longest corolla-lobes; sepals minute to foliaceous.  
 Corolla-lobes triangular-falcate, less than twice as long as wide.  
 Corolla-lobes linear-falcate, usually 3-5 times as long as wide.  
 \*Sepals broad and flat, exceeding the hypanthium, contiguous or nearly so at base, separated by narrow, acute or barely rounded sinuses.
- Leaves cinerous on the veins beneath, nearly or quite glabrous above, even when young.  
 Sepals black beneath the tomentum; leaves obtuse, rounded at the base.  
 Sepals green beneath the tomentum; leaves sharply acute.  
 Sepals ovate, 7-8 mm. wide, broadly overlapping; leaves obtuse at base, on petioles about 1 cm. long.  
 Sepals oblong, not over 4 mm. wide, not overlapping; leaves acute at base.  
 Sepals finely denticulate, broadest above the base.  
 Sepals entire, tapering regularly from the base.
- Leaves ferruginous on the veins beneath, thick and firm, freely stellate-pubescent above when young, somewhat so when mature; sepals thickly ferruginous-tomentose.  
 Leaves of an oblong type, broadest at or above the middle, acute at base.  
 Leaves obtuse, 4-5 cm. wide.
1. *C. Mandonis*  
 2. *C. gloriosus*  
 3. *C. Brittonianus*  
 4. *C. magnificus*  
 5. *C. unduavensis*  
 6. *C. Hartwegi*  
 7. *C. latisepalus*  
 8. *C. Caoutchouc*  
 9. *C. aurantiacus*  
 10. *C. fulvus*

- Leaves acuminate, 2-3 cm. wide. 11. *C. Weberbaueri*
- Leaves of an ovate type, broadest well below the middle, rounded at base, acute or sub-acuminate; sepals spreading or reflexed. 12. *C. rufus*
- \*\*Sepals triangular to linear, equaling or shorter than the hypanthium, 1.5-6 mm. long. (In case of doubt, species with more or less spreading and therefore conspicuous sepals have been placed in the next division, and those with appressed inconspicuous sepals here.) (See also \*\*\*)
- Sepals triangular, notably broadened to the base and therefore separated by acute sinuses; leaves distinctly rounded and obtuse at the apex. 13. *C. ellipticus*
- Sepals linear, with flat sinuses.
- Leaves narrowly oblong to lanceolate or linear, rarely exceeding 2 cm. in width; sepals 1-3 mm. long.
- Leaves densely ferruginous-tomentose beneath, the actual surface virtually concealed.
- Peduncles 5-8 cm. long; upper corolla-lobes 10-12 mm. long. 14. *C. longifolius*
- Peduncles 1-2 cm. long, much shorter than the subtending leaves; upper corolla-lobes 8 mm. long. 15. *C. intonsus*
- Leaves thinly tomentose to sparsely stellate beneath, the actual surface visible through the indument.
- Leaves acuminate at the apex.
- Blades lanceolate, about 4 times as long as wide. 16. *C. Jahni.*
- Blades linear, about 8 times as long as wide. 17. *C. lanceolatus*
- Leaves acute or obtuse.
- Filaments tomentose; leaves repand-denticulate. 18. *C. ferrugineus*
- Filaments glabrous; leaves merely callos-denticulate. 19. *C. barbatellus*
- Leaves of a broader type, regularly exceeding 2 cm. in width.
- Serrations of the leaves 5-8 mm. long; blades ovate, acuminate, cuneate to a slender petiole. 20. *C. australis*
- Serrations of the leaf minute.
- Sepals 5-6 mm. long; hypanthium minutely wing-angled.

- Peduncles densely tomentose; petioles 3-5 cm. long; leaf-blades elliptic or oblong, about twice as long as wide. 21. *C. foliosus*
- Peduncles almost or quite glabrous; petioles 1-2 cm. long; leaf-blades broadly round-ovate. 22. *C. alatus*
- Sepals 1-3 mm. long; hypanthium densely tomentose.
- Leaves rounded or subcordate at base. 23. *C. subcordatus*
- Leaves narrowed to the base.
- Leaf-blades 5-8 cm. long, obtuse or subacute. 24. *C. salviaeformis*
- Leaf-blades 15-20 cm. long, tapering regularly from the middle to both ends. 25. *C. nervosus*
- \*\*\*Sepals linear, exceeding the hypanthium, (6-)7.5-30 mm. long.
- Sepals less than 10 mm. long.
- Corolla at least 40 mm. long over all.
- Leaves obtuse or rounded; stem very densely rough-tomentose.
- Leaves obovate, 6-10 cm. long; corolla densely tomentose externally. 26. *C. comosus*
- Leaves elliptic, less than 4 cm. long; corolla sparsely stellate-pubescent externally. 27. *C. hirsutus*
- Leaves acute to subacuminate, ample; stem closely tomentose. 28. *C. cinereus*
- Corolla 25-30 mm. long over all.
- Sepals densely stellate-tomentose, the surface hidden, entire or with 1 or 2 low teeth only; leaves narrowed to the base.
- Leaves acute, about twice as long as wide. 29. *C. suberianthus*
- Leaves obtuse or subacute, 3-4 times as long as wide. 30. *C. Lindenianus*
- Sepals thinly stellate-pubescent, the surface visible.
- Leaves elliptic, cuneate or subacuminate to the base. 31. *C. licayensis*
- Leaves oblong, obtuse to rounded at the base.
- Sepals entire; hairs of the peduncle 2 mm. long. 32. *C. occultus*
- Sepals prominently and saliently toothed; hairs on the peduncle less than 1 mm. long.
- Leaves oblong-ovate, broadest below the middle, long-acuminate. 33. *C. Preslii*

- Leaves oblong-obovate, broadest above the middle, acute. 34. *C. Featherstonei*
- Sepals more than 10 mm. long.  
 Sepals densely ferruginous, more or less involute.  
 Leaves prominently serrate, about 3-4 times as long as wide, not more than 10 cm. long, rounded to broadly obtuse at base. 35. *C. erianthus*
- Leaves minutely denticulate, about twice as long as wide, 12-18 cm. long, acute at base. 36. *C. pichinchensis*
- Sepals flat.  
 Veins almost completely obscured on the lower leaf-surface by the dense tomentum. 37. *C. verbascifolius*
- Veins prominent on the lower leaf-surface, merely marked by tomentum.  
 Sepals 12-15 mm. long; leaves elliptic-rhomboid, cuneate from above the middle to the base. 38. *C. Macbridei*
- Sepals 25-30 mm. long; leaves oblong, rounded at the base. 39. *C. perlongus*

1. CENTROPOGON MANDONIS Zahlbr. Ann. Naturh. Hofmus. Wien 6: 438. 1891.

*Mandon 494*, Prov. Larecaja, Bolivia.

2. CENTROPOGON GLORIOSUS (Britton) Zahlbr. Bull. Torrey Club 24: 373. 1897.

*Siphocampylus gloriosus* Britton, Bull. Torrey Club 19: 373. 1892.

*Rusby 647* (type), Unduavi, Bolivia; *Rusby 645*, Sorata, Bolivia; *Bang 2620* (Bolivia); *Buchtien 471* (Herb. N. Y. Bot. Gard.), Unduavi; *Buchtien 735*, Unduavi; *Buchtien 736* (National Herb.), Unduavi.

3. CENTROPOGON BRITTONIANUS Zahlbr. Bull. Torrey Club 24: 373. 1897.

*Siphocampylus giganteus latifolius* Britton, Bull. Torrey Club 19: 373. 1892.

*Rusby 638* (type), Unduavi, Bolivia; *Bang 738*, Yungas, Bolivia; *Buchtien*, Unduavi; *Buchtien 471* (Gray Herb.), Unduavi; *Buchtien 736* (Herb. N. Y. Bot. Gard., National Herb.), Unduavi.

4. CENTROPOGON MAGNIFICUS Zahlbr. & Rech. Med. Rijks Herb. 13: 50. 1913.

*Steinbach 5011*, Dept. Cochabamba, Bolivia.

5. *CENTROPOGON UNDUAVENSIS* (Britton) Zahlbr. Bull. Torrey Club 24: 374. 1897.

*Siphocampylus unduavensis* Britton, Bull. Torrey Club 19: 373. 1892.

Rusby 649 (type), Unduavi, Bolivia; *Buchtien* 128, 733, 3016, Unduavi.

6. *CENTROPOGON HARTWEGI* (Benth.) Benth. & Hook. f.; B. D. Jackson, Ind. Kew. 4: 1274. 1895.

*Siphocampylus Hartwegi* Benth. Pl. Hartw. 139. 1844.

*Hartweg* 777 (type), Loxa, Ecuador.

7. *Centropogon latisepalus* n. sp.

Stem apparently shrubby, strongly angled and flattened, densely cinereous-tomentose when young, becoming thinly tomentose 3 dm. from the summit; internodes 15-20 mm. long; petioles stout, 8-10 mm. long, tomentose like the stem; leaf-blades spreading, thin and membranous, broadly elliptic-oblong, 8-11 cm. long, 4.5-5 cm. wide, the uppermost a trifle smaller, sharply acute or subacuminate, minutely denticulate with low, salient, callous, triangular teeth (6-7 teeth per cm. of margin, 0.2 mm. high), broadly cuneate or obtuse at base, above very thinly stellate-pubescent on the surface, or glabrous with age, densely brown-stellate along the midvein and lower portion of the laterals, beneath softly and thinly stellate on the surface and densely so on the principal veins with cinereous tomentum; lateral veins 15-18 pairs, broadly ascending, conspicuously arcuate; peduncles axillary, ascending, stout, 7-8 cm. long, densely cinereous-tomentose, subulate-bracteolate near the base; hypanthium broadly depressed-hemispheric, 8 mm. high, 12 mm. wide when pressed, closely but densely cinereous-tomentose; sepals erect, foliaceous, ovate-elliptic or ovate, 18 mm. long, 7-8 mm. wide, broadly overlapping, short-acuminate, thinly stellate on the back, inconspicuously reticulate, the exposed margin denticulate like the leaves, the concealed margin sub-entire; sinuses narrow, acute; corolla red, cinereous-stellate or subtomentose, the tube 40 mm. long, the lobes linear-falcate, strongly decurved, the upper about 9 mm., the lateral about 6, the lower 4 mm. long; filaments thinly pilose, exerted 6 mm.; anther-tube 7 mm. long, strongly hirsute on the connectives on the distal half, the two lower anthers bearded.

TYPE: *Pittier* 739, collected Dec. 1905, Cuestá de Tocotá, road from Buenaventura to Cali, Dept. El Valle, Colombia, altitude 1500-1900 m., and deposited in the herbarium of the New York Botanical Garden.

8. *Centropogon Caoutchouc* (H.B.K.) n. comb.

*Lobelia Caoutchouc* H.B.K. Nov. Gen. & Sp. 3: 304. 1818.

*Centropogon luteus* Wimmer, Repert. Spec. Nov. 19: 247. 1924.

*Humboldt & Bonpland* (type), Popayan Andes; *Goudot; Linden 1072* (type of *C. luteus* Wimmer), Quindio; *Pennell 8872*, near Salento, Dept. Caldas, alt. 2100-2500 m., 25-31 July 1922; *Killip & Hazen 9561*, between Rio Toche and "Machin," Old Quindio Trail, Dept. Tolima, alt. 2000-2500 m., 3 Aug. 1922.

9. *Centropogon aurantiacus* n. sp.

Stem shrubby, closely stellate-tomentose above, becoming glabrous 3 dm. from the summit, internodes 2-5 cm. long; petioles slender, 10-13 mm. long, thinly tomentose; leaf-blades firm, elliptic, the largest 85 mm. long, 35 mm. wide, sharply acute or abruptly short-acuminate, obtuse or rounded at the base, subentire or minutely denticulate with low, black, callous, salient teeth (about 6 teeth per cm. of margin, 0.3 mm. high), the upper surface thinly and minutely stellate, with inconspicuous veins, the lower surface thinly but conspicuously stellate and densely cinereous-tomentose on the prominently reticulate veins; lateral veins about 10 pairs, strongly ascending; peduncles axillary, 5-6 cm. long, equaling the subtending leaves, thinly stellate-tomentose; hypanthium hemispheric, 8 mm. long, 13 mm. wide when pressed, 10-ribbed, closely and densely ferruginous-tomentose; sepals erect, linear, 17 mm. long, 2 mm. wide, tapering regularly to the tip, entire, 1-nerved, inconspicuously reticulate, thinly stellate, especially at the margin, separated by broadly rounded sinuses 2 mm. wide; corolla orange-red, thinly stellate, the tube 30 mm. long, the lobes strongly falcate and decurved, the upper 9 mm. long, the lateral and lower much shorter; filaments exerted 5 mm., thinly hirsute; anther-tube 7 mm. long, densely hirsute on the connectives, the two lower anthers bearded.

TYPE: *Killip & Hazen 9623*, collected 3 Aug. 1922, between "El Eden" and "La Palmilla," Old Quindio Trail, Dept. Tolima, Colombia, altitude 1800-2300 m., and deposited in the herbarium of the New York Botanical Garden. Other collections are *Spruce 5576*, Ecuador, and *Heilborn 453*, Garnetas, Ecuador.

10. *Centropogon fulvus* n. sp.

Stem shrubby, climbing, strongly angled and flattened above, closely brown stellate-tomentose when young, glabrescent in age, the internodes 15-20 mm. long; petioles stout, 1-2 cm. long, tomentose like the stem; leaf-blades firm, narrowly elliptic-



obovate to elliptic-oblong, broadest at or above the middle, the largest 5 by 14 cm., the upper gradually reduced, obtuse, or rounded and minutely apiculate, finely denticulate (about 8 teeth per cm. of margin) with low, black, callous, triangular, salient teeth 0.3 mm. long and not surpassing the tomentum, cuneate or subacute at base, upper surface dull green with prominently impressed veins, thinly ferruginous-stellate when young, glabrous at maturity, the mid-vein and lower part of the laterals permanently and densely tomentose, lower surface closely ferruginous-tomentose, especially on the veins; lateral veins 16-22 pairs, arcuately ascending, the veinlets conspicuously reticulate; peduncles axillary, slender, 7-8 cm. long, shorter than the subtending leaves, strongly angled, tomentose like the stem; hypanthium broadly hemispheric, strongly ribbed, 7 mm. high, 14 mm. wide when pressed, densely tomentose; sepals erect, elliptic-oblong, 11-14 mm. long, 4-5 mm. wide, acute, tapering to a base 2 mm. wide, with about 6 black callous teeth on each side, densely and closely tomentose within and without, separated by narrow rounded sinuses; corolla purple-red, densely tomentose with orange-colored stellate hairs, the tube 30 mm. long, the lobes narrowly triangular-falcate and decurved, the upper 9 mm. long, the lower much shorter; filaments villous, especially on the ventral side, not exserted; anther-tube 8 mm. long, densely hirsute on the fissures distally with orange-colored hairs, the two lower anthers bearded.

TYPE: *Pennell & Killip 7382*, collected 28 June 1922, at "San Jose," San Antonio, Dept. El Cauca, altitude 2400-2700 m., and deposited in the herbarium of the New York Botanical Garden.

11. *CENTROPOGON WEBERBAUERI* Zahlbr. Bot. Jahrb. 37: 453. 1906.

*Weberbauer 3247* (type, not 3347, as cited by Zahlbr.), Huamalies, Peru.

12. *CENTROPOGON RUFUS* Wimmer, Repert. Spec. Nov. 19: 249. 1924.

*Macbride 4473*, Tambo de Vaca, Peru.

13. *Centropogon ellipticus* n. sp.

Stem herbaceous, strongly angled and flattened above, densely tomentose when young with dark brown, stellate hairs, becoming glabrous 3-4 dm. from the summit, the internodes 2-3 cm. long; petioles stout, 8-12 mm. long, tomentose like the stem; leaf-blades firm, elliptic, the largest 12 cm. long, 4.5 cm. wide,

rounded at the apex, entire or with minute black intramarginal teeth, rounded to broadly obtuse at base, thinly stellate above when young with dark brown hairs, glabrescent at maturity on the surface, persistently tomentose on the midvein and base of the lateral veins, thinly tomentose beneath on the surface and densely so on the veins with ferruginous branched hairs; lateral veins about 16 pairs, slightly arcuate, ascending, veinlets inconspicuously reticulate; peduncles axillary, stout, ascending or nodding at the tip, 6-7 cm. long, shorter than the subtending leaves, tomentose like the stem; hypanthium broadly hemispheric, 7-8 mm. high, 12 mm. broad when pressed, conspicuously ribbed, densely stellate-tomentose; sepals erect, broadly triangular with concave sides, 3-4 mm. long and wide, densely tomentose; corolla orange, the lobes yellow within, thinly stellate-tomentose, the tube 23 mm. long, the upper lobes 9 mm., the lower 5 mm. long; filaments glabrous, exerted 5 mm.; anther-tube 6 mm. long, glabrous, the two lower anthers bearded.

TYPE: *Pennell 2486*, collected 13-15 Oct. 1917, near Sibate, Dept. Cundinamarca, Colombia, altitude 2900-3000 m., and deposited in the herbarium of the New York Botanical Garden. Other collections are *Holton*, Bogota; *Pennell 2419*, El Peñon, near Sibate, 13 Oct. 1917; *Pennell 9232*, "Pinares" above Salento, Dept. Caldas, alt. 2600-2900 m., 2-10 Aug. 1922; and *Killip & Bro. Ariste-Joseph 11,941*, Paramo de Choachi, near Bogota, 3700 m., 8 Aug. 1922.

14. *CENTROPOGON LONGIFOLIUS* Wimmer, Repert. Spec. Nov.  
19: 246. 1924.

*Siphocampylus barbatus* Benth. Pl. Hartw. 139. 1844.

*Matthews 1186* (type), Huanacabra, Peru; *Jameson 18*; *Hitchcock 21,616*, Prov. Azuay, Ecuador; *Macbride 4445*, Tambo de Vaca, Peru; *Hartweg 778* (type of *S. barbatus* Benth.), Loxa, Ecuador.

15. *Centropogon intonsus* n. sp.

Stems woody, hollow, strongly angled and more or less compressed above, densely and coarsely ferruginous-tomentose when young, glabrous in age, the internodes very short; petioles stout, 4 mm. long, tomentose like the stem; leaf-blades narrowly oblong, thick and firm, 30-55 mm. long, 7-14 mm. wide, acute at both ends, denticulate with black, callous, barely salient, mostly intramarginal teeth, the upper surface rugulose, dull green, thinly fulvous-stellate, particularly at the margin, with deeply impressed veins, the lower surface densely and persistently ferruginous-tomentose, especially on the 8-12 pairs of arcuately ascending

lateral veins; peduncles axillary, slender, 1-2 cm. long, much shorter than the subtending leaves, pubescent like the stem; hypanthium urceolate-hemispheric, 3 mm. high, 5 mm. wide when pressed, densely tomentose; sepals broadly triangular, 1 mm. long and wide, mucronate, entire, densely tomentose, separated by broad flat sinuses; corolla red, thickly ferruginous-stellate, the tube 28 mm. long, the lobes linear-falcate, decurved, the upper 8 mm. long, the lower shorter; filaments exerted about 7 mm., rather densely villous with short white hairs; anther-tube 5 mm. long, sparsely pilose with short pale hairs, the two lower anthers conspicuously bearded.

TYPE: *Rose, Pachano & Rose 23,173*, collected 28 Sep. 1918, near Las Juntas, Ecuador, and deposited in the United States National Herbarium.

16. *Centropogon Jahnii* n. sp.

Stems apparently herbaceous, strongly angled and flattened, thinly stellate above, soon becoming glabrous, the internodes about 1 cm. long; petioles slender, 1 cm. long, thickly stellate dorsally; leaf-blades thin, dull green, lanceolate, 6-8 cm. long, 15-22 mm. wide, gradually tapering to a sharply acute or sub-acuminate tip, acute or subcuneate at base, finely and sharply serrulate, the serrations tipped with black, callous teeth, somewhat roughened above with thin stellate pubescence, particularly on the veins, sparsely stellate beneath; lateral veins faint, irregularly ascending, about 12 pairs, the veinlets reticulate; peduncles axillary, slender, 5-6 cm. long, sparsely stellate below, nearly glabrous above; hypanthium depressed-hemispheric, 4 mm. long, 7 mm. wide when pressed, thinly stellate; sepals erect, appressed, triangular, 1.5-2 mm. long, acute, entire, sparsely stellate, separated by broad flat sinuses; corolla red, tipped with yellow, very sparsely stellate, the tube 35 mm. long, the lobes linear-falcate, decurved, the upper 8 mm. long, the lower shorter; filaments exerted 3 mm., minutely villous; anther-tube 7 mm. long, sparsely pilose with long white hairs, the two lower anthers bearded.

TYPE: *Jahn 917*, collected 21 Jan. 1922, on the Páramo de Canaguá, Mérida, Venezuela, altitude 2500 m., and deposited in the United States National Herbarium. A second collection is *Jahn 916*, of the same place and date.

17. *CENTROPOGON LANCEOLATUS* Wimmer, Repert. Spec. Nov.  
19: 245. 1924.

*Jahn 1025*, Páramo de Aricagua, Mérida, Venezuela.

18. *Centropogon ferrugineus* (L.f.) n. comb.

*Lobelia ferruginea* L.f. Suppl. 394. 1781.

*Lobelia barbata* Cav. Icon. 6: 12. pl. 519. 1801.

*Siphocampylus ferrugineus* G. Don, Gen. Syst. 3: 701. 1834.

*Siphocampylus barbatus* G. Don, l.c. 1834.

*Centropogon barbatus* Planch. Flore Serres 6: 16. 1850-1851.

Colombia, without detail of locality: *Bonpland*, *Triana* 1574, 1575, *Dawe* 347; vicinity of Bogota; *Ariste-Joseph*, *Holton* 407, *Parseval-Grandmaison*, *André* 721, *Purdie*, *Triana* 69; *Páramo Oruiza*: *Purdie*; *Guasca*: *Ariste-Joseph*; Dept. Caldas: *Dawe* 745; Dept. Cundinamarca: *Pennell* 1933.

*Centropogon ferrugineus parviflorus* (Zahlbr.) n. comb.

*Centropogon barbatus parviflorus* Zahlbr. Ann. Naturh. Hofmus.

Wien 6: 436. 1891.

*André* 4004, Ecuador; *Heilborn* 715, Ecuador.

19. *Centropogon barbatellus* n. sp.

Stems woody, possibly climbing, strongly grooved, densely stellate above with pale brown tomentum, becoming glabrous 3-4 dm. from the summit, the internodes 5-10 mm. long; petioles stout, 5-8 mm. long, densely stellate-tomentose; leaf-blades thin, narrowly oblong or elliptic-oblong, 4-8 cm. long, 1-2.5 cm. wide, acute or subacuminate, obtuse to broadly acuminate at the base, minutely denticulate with low, broadly triangular, salient, callous teeth (about 5 teeth per cm. of margin, 0.4 mm. high), varying to entire, thinly stellate above when young, particularly along the plane midvein, becoming glabrous at maturity, permanently stellate beneath with cinereous hairs, especially along the veins; lateral veins about 12 pairs, arcuately ascending, hardly apparent above, the veinlets obscure; peduncles axillary, slender, 25-40 mm. long, exceeding the subtending leaves, thinly stellate-tomentose; hypanthium broadly hemispheric, 5 mm. high, 8 mm. wide when pressed, densely and closely stellate-tomentose; sepals erect, narrowly triangular, 3 mm. long, 1 mm. wide at the base, entire, thinly tomentose, separated by broad flat sinuses; corolla red without, yellow within, thinly and sparsely stellate, the tube 25 mm. long, the lobes narrowly falcate and depressed, the upper 7 mm., the middle 5 mm., the lower 4 mm. long; filaments exserted about 10 mm., glabrous; anther-tube nearly straight, black, glabrous, the two lower anthers strongly bearded.

TYPE: *Pennell* 3115, collected 15-17 Dec. 1917, at "Rosálito," near *Páramo de Ruiz*, Dept. Tolima, Colombia, altitude 2900-3200 m., and deposited in the herbarium of the New York

Botanical Garden. Other collections are *Triana 1577*; *Schlim 420*; and *Pennell 9233*, "Pinares" above Salento, Dept. Caldas, alt. 2600-2900 m., 2-10 Aug. 1922.

20. *Centropogon australis* (Wimmer) n. comb.

*Centropogon grandidentatus australis* Wimmer, Repert. Spec. Nov. 19: 245. 1924.

*Funcke 1062* (type), Venezuela; *Linden 404*, Venezuela. The similarity in leaf-form between this species and *C. grandidentatus* (Schlecht.) Zahlbr. is striking, but the Mexican species is not stellate-pubescent.

21. *CENTROPOGON FOLIOSUS* Rusby, Descr. S. Am. Pl. 146. 1920.

*Smith 1385* (type), Santa Marta, Colombia.

22. *Centropogon alatus* n. sp.

Stems strongly angled and more or less flattened, thinly stellate above, soon becoming glabrous, the internodes 5-20 mm. long; petioles slender, strongly flattened, dilated at the base, thinly stellate, 1-2 cm. long; leaf-blades broadly round-ovate, thin, 5-7 cm. long, 3.5-5 cm. wide, subacuminate to a rounded and mucronate tip, broadly rounded below to an abruptly cuneate base, sharply and prominently spinulose-denticulate (5 or 6 teeth per cm. of margin, 0.5 mm. long), upper surface dark green, thinly pubescent with scattered, simple or sparingly branched hairs, lower surface thinly stellate with cinereous hairs; lateral veins 8-12 pairs, spreading almost at right angles, crooked, irregularly arcuate, the veinlets reticulate; peduncles axillary, slender, 5-6 cm. long, almost glabrous, bibracteolate near the base; hypanthium broadly hemispheric, 5 mm. high, 9 mm. wide when pressed, thinly stellate, narrowly 10-winged; sepals triangular, dilated at base, 5 mm. long, 2 mm. wide, acute, with 1 or 2 prominent teeth, thinly stellate; corolla red, the tube 30-35 mm. long, almost glabrous, the lobes linear-falcate, strongly decurved, the upper 10 mm., the lower 8 mm. long; filaments barely exerted, sparsely pubescent; anther-tube 8 mm. long, glabrous, the two lower anthers bearded.

TYPE: *Jahn 1026*, collected 31 Mar. 1922, on the Páramo de Aricagua, Mérida, Venezuela, altitude 2000 m., and deposited in the United States National Herbarium.

23. *CENTROPOGON SUBCORDATUS* Zahlbr. Repert. Spec. Nov. 14: 140. 1915.

*Sodiolo 91/4* (type), Palmira, Ecuador; *Jameson 102*; *Pennell 10,468*, Cerro Tatama, Dept. Caldas, Colombia, alt. 2000-3000 m.; *Macbride 2125*, Huanuco, Peru.

24. *CENTROPOGON SALVIAEFORMIS* Zahlbr. Repert. Spec. Nov.  
14: 138. 1915.

*Sodi* 91/5 (type), Cavaron, Ecuador; *Heilborn* 453, Ecuador.

25. *Centropogon nervosus* Wimmer, n. sp.

Stem shrubby, strongly angled and flattened above, thinly stellate-tomentose with cinereous hairs, soon glabrescent, the internodes 5-10 mm. long; petioles slender, 15-25 mm. long, pubescent like the stem, eventually becoming glabrous; leaf-blades thin, elliptic-rhomboid, broadest near the middle, 21 cm. long, 7 cm. wide, the upper gradually reduced, tapering regularly to an acute or subacuminate apex, cuneate to the base, sharply and minutely denticulate (about 8 teeth per cm. of margin) with black, callous, salient teeth 0.2-0.3 mm. long, both surfaces thinly stellate with cinereous hairs, more densely along the veins; lateral veins numerous, 4-5 mm. apart, almost straight, ascending at an angle of 70°, the veinlets finely reticulate; peduncles axillary, stout, 4-5 cm. long, densely cinereous-tomentose; hypanthium broadly hemispheric, 4 mm. high, 7 mm. wide when pressed, densely cinereous-tomentose; sepals erect or appressed, narrowly triangular, 3 mm. long, 1.5 mm. wide, acute, entire, thinly stellate, the sinuses broad and flat; corolla red, densely tomentose, the distal portion and anthers lacking.

TYPE: *Cook & Gilbert* 1347, collected 19 June 1915, in the Lucumayo Valley, Peru, altitude 1800-3600 m., and deposited in the United States National Herbarium.

Strongly suggestive of *C. foliosus* Rusby in its leaf-form, and of *C. verbascifolius* (Presl) Gleason and *C. Macbridei* Gleason in its venation, but differing from both in the short sepals. The species was first recognized as distinct by Wimmer, who examined the type specimen and suggested the name; the description above is my own.

26. *Centropogon comosus* n. sp.

Stem shrubby, strongly angled and somewhat flattened, densely and coarsely cinereous-tomentose with stellate hairs above, somewhat smoother below, the internodes about 1 cm. long; petioles stout, 15-30 mm. long, tomentose like the stem; leaf-blades thick and firm, elliptic-obovate, the largest 9 cm. long and 5 cm. wide, the upper somewhat reduced, rounded to broadly obtuse and sometimes minutely apiculate at the apex, broadest near the middle or somewhat above it, subcuneate to an obtuse base, entire or minutely denticulate with barely salient teeth (about 6 teeth per cm. of margin, 0.2 mm. long), but apparently ciliate by the projecting tomentum, the upper

side dull green, slightly rugose, and permanently scabrellate with stellate hairs, especially along the midvein, the lower side roughly and densely tomentose with cinereous branched hairs, especially along the veins; lateral veins 10-14 pairs, widely divergent, barely arcuate, somewhat impressed above, strongly elevated beneath, the veinlets reticulate; peduncles axillary, stout, ascending, 6-8 cm. long, tomentose like the stem; hypanthium broadly hemispheric, 6 mm. high, 12 mm. broad when pressed, densely and coarsely stellate-tomentose; sepals linear, erect, 9 mm. long, entire, densely stellate-tomentose, separated by broadly rounded sinuses; corolla probably red, but the surface entirely concealed by heavy, coarse, rough, brown, stellate tomentum, the tube 38 mm. long, the lobes narrowly linear-falcate, strongly decurved, the upper 10 mm. long, the lower shorter; filaments sparsely villous, exerted 5-7 mm.; anther-tube 8-9 mm. long, sparsely pilose with a few long hairs in the fissures, especially dorsally, the two lower anthers bearded.

TYPE: *Hitchcock 21,545*, collected 7 Sep. 1923, between San Lucas and Oña, province of Loja, Ecuador, altitude 2200-3100 m., and deposited in the herbarium of the New York Botanical Garden. Another collection is *Rose, Pachano & Rose 23,151*, from Zaragura, Ecuador.

### 27. *Centropogon hirsutus* n. sp.

Stems apparently shrubby, densely stellate-tomentose above with dark brown hairs, the upper internodes 1-2 cm. long; petioles stout, 4-8 mm. long, tomentose like the stem; leaf-blades firm, dark green, broadly elliptic, 3-3.5 cm. long, 13-18 mm. wide, broadest about the middle, broadly rounded and callous-apiculate at the apex, rounded or broadly obtuse at base, remotely and minutely denticulate with black callous teeth (about 5 teeth per cm. of margin, 0.2-0.3 mm. high), thinly stellate on the midvein above when young, glabrous on the surface, beneath pale green, the prominently reticulate veins mostly concealed by the persistent, somewhat floccose, dark brown, stellate tomentum; peduncles axillary, stout, erect, 6-7 cm. long, twice as long as the subtending leaves, densely brown-tomentose; hypanthium deeply hemispheric, 7 mm. high, 9 mm. wide when pressed, obscurely angled, densely brown-tomentose; sepals erect or somewhat spreading, linear, 7-8 mm. long, acuminate to a black callous tip, remotely callous-denticulate, thinly and irregularly stellate; corolla red, sparsely and thinly stellate, the tube 30 mm. long, 10 mm. wide at the throat, the lobes linear-falcate, strongly decurved, the upper 13 mm., the lower 11 mm. long; filaments barely exceeding the corolla, nearly glabrous; anther-tube 8 mm. long, somewhat pubescent at the base, the two lower anthers bearded.

TYPE, *Dawe 743*, collected 1918, Dept. Caldas, Colombia, and deposited in the herbarium of the New York Botanical Garden.

28. *Centropogon cinereus* n. sp.

Stems shrubby, climbing, channelled above and densely pubescent with ferruginous branched hairs, becoming terete and glabrous with age; internodes elongating to 2-3 cm. long; petioles slender, flattened, densely tomentose, 15-30 mm. long; blades thin, broadly elliptic, the largest 18 cm. long by 9 cm. wide, the upper smaller, seldom exceeding 10 cm. long by 5 cm. wide on the terminal two decimeters of stem, sharply acute or sub-acuminate, minutely denticulate (7-9 teeth per cm. of margin) with low (0.5 mm.), black, callous, salient, sharply triangular teeth, broadly cuneate at base, upper surface dull green, ferruginous with stellate hairs when young, becoming glabrous on the surface at maturity, tardily glabrescent on the midvein, lower surface stellate-tomentulose on the surface, stellate-tomentose on the principal veins; lateral veins 16-20 on each side, prominent beneath, lightly impressed above, ascending and gently arcuate; peduncles from the upper axils, 1-2 cm. long, slender, densely ferruginous-tomentose; hypanthium broadly hemispheric, 5 mm. high, 8 mm. wide when pressed, densely ferruginous-tomentose; sepals erect, linear, 7-8 mm. long, entire, thinly tomentose, separated by flat sinuses wider than the sepals; corolla red, ferruginous-tomentulose, the tube 35 mm. long, the upper lobes about 12 mm. long, the laterals about 6, the lower about 4; filament-tube exerted about 9 mm., thinly pubescent; anther-tube 8 mm. long, strongly pilose on the fissures distally, the two lower anthers bearded.

TYPE: *Pennell 10,724*, collected 18-19 Sep. 1922 at "Buenos Aires," north of Supia, Dept. Caldas, Colombia, altitude 2000-2300 m., and deposited in the herbarium of the New York Botanical Garden. Other examples are *Pennell 10,743*, same date and locality, *Triana 84*, Quindio; *Jervise* without number, Quindio.

29. *CENTROPOGON SUBERIANTHUS* Zahlbr. Repert. Spec. Nov.  
14: 134. 1915.

*Lehmann 5932* (type), Popayan Andes, Colombia.

30. *CENTROPOGON LINDENIANUS* Wimmer, Repert. Spec. Nov.  
19: 246. 1924.

*Linden 1212* (type), near Bogota, Colombia; *Linden 837*; *Jameson 56, 144*; *Pennell 7089*, "Paletara" to "Calaguala,"



Dept. El Cauca, Colombia, alt. 3000-3200 m., 17 June 1922; Pennell 9375, "Alaska" above Salento, Dept. Caldas, Colombia, alt. 3100-3700 m., 7 Aug. 1922.

31. *Centropogon licayensis* n. sp.

Stem apparently shrubby, densely gray-brown stellate-tomentose above, glabrescent with age, the floriferous internodes much abbreviated; petioles slender, 12-14 mm. long, densely and closely tomentose; blades broadly elliptic, thin and membranous, 8-11 cm. long, 4-5.5 cm. wide, broadest near the middle, sharply acute at the apex, cuneate or subacuminate at the base, minutely but prominently denticulate with black, callous, salient teeth (5-8 teeth per cm. of margin, 0.5 mm. long or less), thinly stellate on the surface, densely so on the midvein above, thinly stellate on the surface, densely so on the midvein and laterals beneath; peduncles axillary, 2-3 cm. long, densely cinereous-tomentose; hypanthium hemispheric, 5 mm. high, 7 mm. wide when pressed, densely cinereous-tomentose; sepals erect, narrowly linear, 8 mm. long, densely stellate, rarely with 1 or 2 callous teeth, the sinuses broadly rounded, wider than the sepals; corolla red, the tube 23 mm. long, rather densely stellate, the lobes linear-falcate, strongly decurved, the upper about 12 mm. long, the lower much shorter; filaments conspicuously and softly villous; anther-tube 6-7 mm. long, sparsely pilose in the fissures, the two lower anthers penicillate.

TYPE: *Rose & Rose 23,837*, collected 28 Aug. 1918, at Huigra, Ecuador, on the Hacienda de Licay, and deposited in the United States National Herbarium.

32. *Centropogon occultus* n. sp.

Stems woody, probably climbing, densely shaggy with dark brown branched hairs when young, becoming glabrous with age, strongly flattened, the floriferous internodes 10 mm. long, later elongating to 5 cm.; petioles stout, 7 mm. long, densely shaggy; leaf-blades firm, oblong, 8-10 cm. long, 3-3.5 cm. wide, broadest near the middle, acute, broadly obtuse to rounded at the base, indistinctly repand, minutely and remotely callous-denticulate, the teeth mostly hidden within the projecting tomentum, upper surface rough with mostly simple, straight, deciduous hairs as much as 1 mm. long, lower surface at first densely shaggy with dull brown branched hairs, later becoming merely thinly stellate, except along the midvein; lateral veins 5-10 mm. apart, faintly impressed above, prominently elevated and almost superficial beneath, crooked, irregularly ascending, the veinlets reticulate; peduncles axillary, 5 cm. long, densely shaggy with brown hairs;

hypanthium deeply hemispheric, 8 mm. high, 9 mm. wide when pressed, prominently angled, densely brown-tomentose; sepals erect, linear, 7 mm. long, thin and flat, densely beset with long brown branched hairs, the sinuses flat, much wider than the sepals; corolla thinly pubescent with long branched hairs, red, the tube 23 mm. long, 8 mm. wide at the throat, upper lobes about 10 mm., the lower about 4 mm. long; filaments exerted 8 mm., glabrous; anther-tube 7 mm. long, thinly hirsute dorsally toward the summit; fruit a densely tomentose dry berry.

TYPE: *Rose, Pachano & Rose 23,945* collected 28 Sep. 1918, at Zaragura, Ecuador, and deposited in the United States National Herbarium.

33. CENTROPOGON PRESII Wimmer, Repert. Spec. Nov. 19: 248. 1924.

*Spruce 5022* (type), Ecuador; *Hall*, valley of Baños, Ecuador; *Pachano 214, 215, 216*, Ambato, Ecuador.

34. *Centropogon Featherstonei* n. sp.

Stem climbing, 3-7 m. long, suffruticose or shrubby, densely and coarsely tomentose above with ferruginous branched hairs, eventually glabrescent, the floriferous internodes less than 1 cm. long, becoming 2-3 cm. long at maturity; petioles stout, densely tomentose, 6-8 mm. long; blades soft when pressed, apparently somewhat succulent when fresh, oblong, the largest 11 cm. long by 4 cm. wide, the upper a third smaller, broadly rounded at the base, then gradually expanding with straight or concave sides to the maximum width above the middle, thence sharply acute or subacuminate to the apex, sharply and finely denticulate (about 8 teeth per cm. of margin) with low (0.5 mm.), sharp, callous, salient teeth, rugulose and thinly stellate-pubescent on the upper surface when young, more densely and permanently so on the midvein, densely, softly, and persistently ferruginous-tomentose on the lower surface; lateral veins about 15-18 on each side, widely divergent, gently arcuate, lightly impressed above, prominently elevated beneath, the veinlets obscure; peduncles from the upper axils, slender, divergent, 6-8 cm. long, somewhat shorter than the subtending leaves, densely ferruginous-tomentose; hypanthium hemispheric, 5 mm. high, 8-10 mm. wide when pressed, somewhat angled, densely ferruginous-tomentose; sepals erect or somewhat spreading, linear, 6-7 mm. long, dark brown or nearly black, with 2 or 3 pairs of black, salient, acicular teeth; corolla-tube 28 mm. long, apparently red, but the surface concealed by dense ferruginous tomentum, the lobes narrow, falcate, depressed, the upper about 10 mm., the lateral about 7, the lower about 5 mm. long; filaments thinly

villous, exerted about 13 mm.; anther-tube 8 mm. long, sparsely pilose distally, the two lower anthers bearded.

TYPE, *Macbride & Featherstone 1605*, collected 8-22 July 1922 at Mito, Peru, altitude about 9000 feet, and deposited in the herbarium of the New York Botanical Garden (dupl. in herb. Field Museum).

35. *CENTROPOGON ERIANTHUS* (Benth.) Benth. & Hook. f.;  
B. D. Jackson, Ind. Kew 4: 1274. 1895.

*Siphocampylus erianthus* Benth. Pl. Hartw. 139. 1844.

*Hariweg 778* (type), Loxa (= Loja), Ecuador; *Triana 1559*; *Rose, Pachano & Rose 23,147*, Zaragura, Ecuador; *Hitchcock 21,376*, Loja, Ecuador; *Mille 360*, Ecuador.

36. *CENTROPOGON PICHINCHENSIS* Zahlbr. Repert. Spec. Nov.  
14: 180. 1915

*Sodiño 91/2* (type), Pichincha, Ecuador; *Macbride 4306*, Muña, Peru.

37. *Centropogon verbascifolius* (Presl) n. comb.

*Lobelia verbascifolia* Presl, Prodr. Monog. Lobel. 38. 1836.

*Siphocampylus verbascifolius* A. DC. Prodr. 7: 402. 1839.

*Matthews*, Peru. Closely resembling the next in leaf-form and venation, but distinguished by the more densely tomentose leaves and by the smaller flowers, with a corolla-tube only 21 mm. long.

38. *Centropogon Macbridei* n. sp.

Stems shrubby, climbing, 5 m. long, irregularly compressed and densely ferruginous with stellate tomentum when young, becoming glabrous with age; floriferous internodes 1-2 cm. long, gradually lengthening at maturity; petioles stout, 9-15 mm. long, densely brown-tomentose; blades spreading or somewhat ascending, thin, elliptic-oblong to elliptic-rhomboid, broadest somewhat above the middle, 10-12 cm. long, 4-4.5 cm. wide, the upper gradually reduced, subacuminate, cuneate from the middle or a little below it to an acute base, conspicuously denticulate (about 7 teeth per cm. of margin) with thick, black, callous, triangular teeth, 0.7 mm. long or less, upper surface rough with stellate pubescence, thinly on the surface, densely along the midvein, especially toward its base, lower surface similarly pubescent on the surface and with rows of crowded hairs on the veins and veinlets; midvein impressed or plane above, stout and

elevated beneath; lateral veins 3-5 mm. part, obscure above, prominulous beneath, gently curved-ascending; peduncles 7-11 cm. long, densely tomentose, minutely subulate-bracteolate near the base; hypanthium broadly hemispheric, 8 mm. high, 12 mm. broad when pressed, somewhat 5-ribbed, densely tomentose; sepals erect or ascending, linear-triangular, 12-15 mm. long, densely pubescent, with a few minute callous teeth, especially in the distal half, separated by flat sinuses 3 mm. wide; corolla orange-red without, yellow within, stellate-tomentose, the tube 35-40 mm. long, constricted above the base, gradually expanding to 10 mm. wide at the throat when pressed, its lobes linear-triangular, strongly decurved-falcate, long-acuminate, more or less involute, the two upper 4-5 mm. wide at base, about 20 mm. long, the lower narrower and shorter; filaments exserted 12-17 mm., straight, puberulous at the throat, becoming pilose or subtomentose with white hairs toward the apex; anther-tube 9-10 mm. long, purplish-brown, glabrous, or with scattered pilose pubescence on the connectives, the two lower anthers bearded; fruit a dry berry.

TYPE: *Macbride 4183*, collected 20 May to 1 June 1923, Huacachi, near Muña, Peru, altitude about 6500 feet, and deposited in the herbarium of the New York Botanical Garden (dupl. in herb. Field Museum); a second collection is *Pennell 7455*, Mount Santa Ana, Dept. El Cauca, Colombia, alt. 2700-3000 m., 29-30 June 1922.

### 39. *Centropogon perlongus* n. sp.

Tall shrub, the stems somewhat flattened above, irregularly angled, densely tomentose with fulvous hairs, glabrescent in age; petioles 15 mm. long, densely tomentose; leaf-blades thin, oblong to oblong-lanceolate, those subtending flowers 11-15 cm. long, 3.5-5 cm. wide, the lower still larger, acute or subacuminate, obtuse to subrotund at base, prominently callous-denticulate (5-8 teeth per cm. of margin) or serrulate, above dark green, thinly fulvous-stellate on the surface, more densely so on the principal veins, beneath pale green, thinly cinereous-stellate on the surface, densely so on the veins; lateral veins 18-22 pairs, slightly arcuate, ascending at angles of 45-70°, impressed above, prominent beneath; peduncles axillary, 13-15 cm. long, densely tomentose, later glabrescent, the bracts linear-subulate, 3 mm. long; hypanthium short-cylindric, 12 mm. long and wide when pressed, strongly angled, densely fulvous-stellate; sepals loosely and irregularly spreading or even reflexed, linear, 25-30 mm. long, 2-3 mm. wide, remotely denticulate with low, black, callous teeth, densely fulvous-stellate on both surfaces, later glabrescent; corolla densely fulvous-tomentose, the tube 42 mm. long, the

lobes all strongly deflexed, the upper pair 22 mm. long; filaments sparsely villous with vertical white hairs; anther-tube 10 mm. long, strongly hirsute in the fissures with yellow hairs, especially distally; berry broadly ellipsoid, 3 cm. long, crowned by the persistent sepals 5-6 cm. long.

TYPE: *Cook & Gilbert 1355*, collected 19 June 1915, in the Lucomayo Valley, Peru, altitude 1800-3600 m., and deposited in the United States National Herbarium. The type is in flower and bud; a second sheet collected the same day exhibits a lower portion of the stem, with fruit and with more elongate leaves.

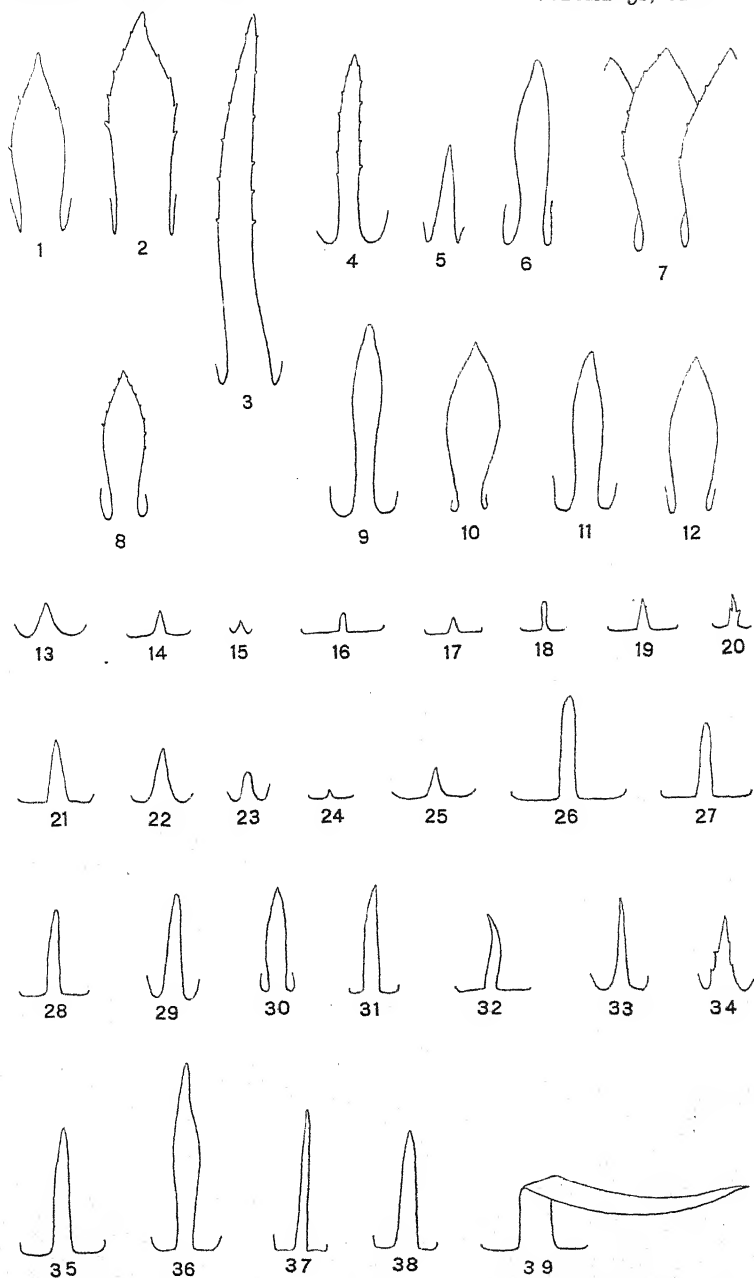
#### ADDITIONAL SPECIES UNKNOWN TO ME

- C. acrodentatus* Wimmer, Repert. Spec. Nov. 19: 241. 1924.  
*C. affinis venezuelanus* Wimmer, l. c. 242. 1924.  
*C. Brittonianus brevidentatus* Zahlbr. & Rech., Med. Rijks Herb. 19: 51. 1913.  
*C. eborinus* Wimmer, l. c. 244. 1924.  
*C. erythraeus* Drake, Jour. de Bot. 3: 237. 1889.  
 ? *C. exasperatus* Presl, Prodr. Monog. Lobel. 48. 1836.  
*C. floccosus* Planch., Flore Serres 6: 16. 1850-51.  
*C. hirtiflorus* Drake, l. c. 239. 1889.  
*C. Karstenii* Zahlbr., Ann. Naturh. Hofmus. Wien 6: 436. 1891.  
*C. macrocarpus* Zahlbr., Bot. Jahrb. 37: 452. 1906.  
*C. rubiginosus* Wimmer, l. c. 249. 1924.

#### Explanation of plate 1

Sepals of stellate-tomentose *Centropogons*,  $\times 1.5$

- |                             |                               |                                |
|-----------------------------|-------------------------------|--------------------------------|
| 1. <i>C. Mandonis</i> .     | 14. <i>C. longifolius</i> .   | 27. <i>C. hirsutus</i> .       |
| 2. <i>C. gloriosus</i> .    | 15. <i>C. intonsus</i> .      | 28. <i>C. cinereus</i> .       |
| 3. <i>C. Brittonianus</i> . | 16. <i>C. Jahnii</i> .        | 29. <i>C. suberianthus</i> .   |
| 4. <i>C. magnificus</i> .   | 17. <i>C. lanceolatus</i> .   | 30. <i>C. Lindenianus</i> .    |
| 5. <i>C. unduavensis</i> .  | 18. <i>C. ferrugineus</i> .   | 31. <i>C. licayensis</i> .     |
| 6. <i>C. Hartwegi</i> .     | 19. <i>C. barbatellus</i> .   | 32. <i>C. occultus</i> .       |
| 7. <i>C. latisepalus</i> .  | 20. <i>C. australis</i> .     | 33. <i>C. Preslii</i> .        |
| 8. <i>C. Caoutchouc</i> .   | 21. <i>C. foliosus</i> .      | 34. <i>C. Featherstonei</i> .  |
| 9. <i>C. aurantiacus</i> .  | 22. <i>C. alatus</i> .        | 35. <i>C. erianthus</i> .      |
| 10. <i>C. fulvus</i> .      | 23. <i>C. subcordatus</i> .   | 36. <i>C. pichinchensis</i> .  |
| 11. <i>C. Weberbaueri</i> . | 24. <i>C. salviaeformis</i> . | 37. <i>C. verbascifolius</i> . |
| 12. <i>C. rufus</i> .       | 25. <i>C. nervosus</i> .      | 38. <i>C. Macbridei</i> .      |
| 13. <i>C. ellipticus</i> .  | 26. <i>C. comosus</i> .       | 39. <i>C. perlongus</i> .      |



STELLATE-TOMENLOSE CENTROPOGONS



## A new fossil species of *Hydrangea*\*

ARTHUR HOLLICK

(WITH PLATE 2)

### *Hydrangea alaskana* n. sp.

Calyx deeply 3-lobed, attached by a common base to a long, slender peduncle; lobes separate, sessile, entire, suborbicular in shape, rounded distally, broadly cuneate proximally, more or less overlapping medianly, varying somewhat in size, 3 or more centimeters in length by 3 or more centimeters in width; nervation pinnate-flabellate, consisting of a straight midvein and three or four secondaries on each side, all of equal rank, that spring from the base and below the median part of the midvein at acute angles of divergence, the inner ones subacrodrome, the outer ones more spreading, occasionally forked or branched, curving upward, connected by irregularly disposed and angled cross nervation, the ultimate ramifications becoming camptodrome in the marginal region. (Pl. 2, Figs. 1, 2.)

Locality: Jaw Mountain, Alaska Peninsula, 20 miles N.W. of Aniakchak Bay.

Formation: Tertiary shaly sandstone.

Collector: W. R. Smith, U. S. Geological Survey. 1922.

FIGS. 1 and 2, which serve to illustrate the species, represent counterparts of a single specimen. This specimen may be seen to include not only the conspicuous sepals of a sterile floret but also, apparently, indications of the remains of a scattered cluster of small fertile flowers. These latter appear to the best advantage in the lower portion of the matrix in FIG. 1; but their identification should be regarded as tentative only.

Reference of our specimen to the genus *Hydrangea* appears to be warranted, as may be seen by comparison with the sterile florets of certain existing species of the genus. A drawing of a normal 4-sepalate specimen of *H. quercifolia* Bartram is introduced for comparison (see FIG. 3); but certain Asiatic species, such as *H. Davidi*, *H. hortensis*, and *H. opuloides*, approach our specimen more nearly in regard to size. Incidentally it may be remarked that our species has only three visible sepals, whereas

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\* Published with the permission of the Director of the U. S. Geological Survey.



the normal number in the sterile florets of existing species is four, or occasionally five. Many, however, present the appearance of being tri-sepalate, for the reason that at least one of the sepals is frequently aborted and is either inconspicuous or early deciduous (see FIG. 4); and in this connection it is of interest to note that of the two figured specimens of the fossil species *Hydrangea Bendirei* (Ward) Knowlton, introduced for comparison, one (see FIG. 5) is shown with four sepals and one (see FIG. 6), apparently, with three.

A number of species, most of them more or less similar to ours, but smaller, from Tertiary horizons in both the Old World and the New, were described and figured under the genera *Getonia*, *Porana*, and *Hydrangea*,\* by various authors, from time to time, and were subsequently shifted from one genus to another by those who studied them more critically. The species cited in the footnote may be regarded as examples of three that simulate ours quite closely and apparently belong in the same generic category.

#### Explanation of plate 2

FIGS. 1, 2. *Hydrangea alaskana* n. sp. Natural size. Specimens in U. S. National Museum, Washington, D. C.

FIGS. 3, 4. *Hydrangea quercifolia* Bartram. Sterile florets, natural size. Alabama, H. Eggert, 1897. Specimens in Herbarium, New York Botanical Garden. (Introduced for comparison.)

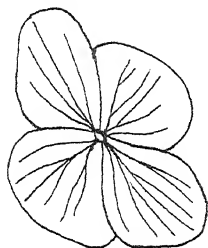
FIGS. 5, 6. *Hydrangea Bendirei* (Ward) Knowlton. U. S. Geol. Survey, Bull. No. 204: pl. 9. f. 6, 7. (Introduced for comparison.)

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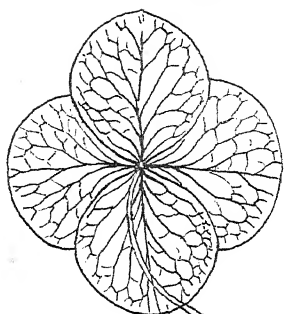
\* *Getonia oeningensis* Unger, *fide* Weber, C.O., Die Tertiarflora der Niederrheinischen Braunkohlenformation. *Paleontographica* 2: 215 [101]. pl. 7. f. 2. 1851 [reprint 1852] (= *Viburnum Weberi* Schenk).

*Porana oeningensis* (Alex. Braun) Heer, *Flora tertiaria Helvetiae* 3: 18. pl. 103. f. 21, 25-28. 1859 (= *Antholithes oeningensis* Alex. Braun).

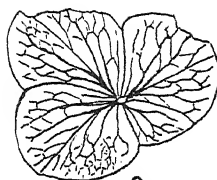
*Hydrangea Bendirei* (Ward) Knowlton, U. S. Geol. Survey, Bull. No. 204 (Fossil flora of the John Day Basin, Oregon): 60. pl. 9. f. 6, 7. 1902 (= *Porana Bendirei* (Ward) Lesquereux = *Marsilea Bendirei* Ward).



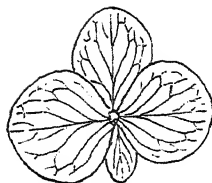
5



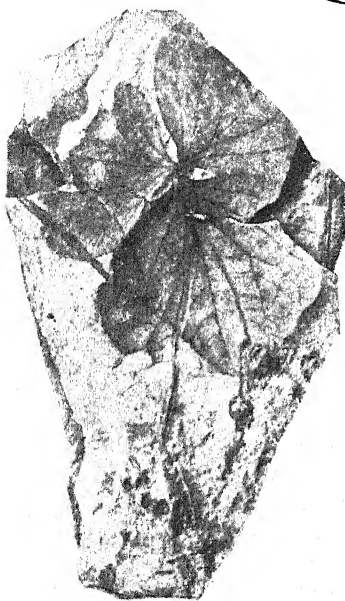
3



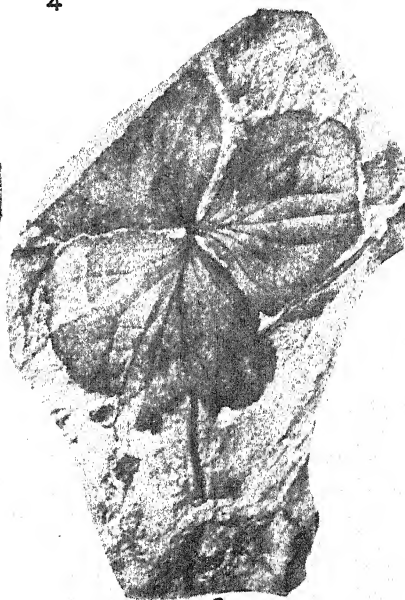
6



4



1



2

NEW FOSSIL SPECIES OF HYDRANGEA



## Application of Gleason's formula to a *Carex lasiocarpa* association, an association of few species\*

EDITH WOOLLETT, DORIS DEAN AND HELEN COBURN

Efforts have been made by Arrhenius, Gleason, and others to find a mathematical expression for the number of species in a given area. These efforts resulted in a formula by Gleason,† based upon intensive and extensive work in associations of a fairly large number of species such as pine and aspen growth and in certain beech-maple areas. The formula is as follows:

If  $A$  is the area of one quadrat,  $B$  is the area of total quadrats,  $C$  is the area under consideration,  $a$  is the average number of species in one quadrat,  $b$  is the total number of species in all quadrats examined, and  $c$  is the total number of species in the area, then

$$\frac{\log B - \log A}{\log C - \log A} = \frac{b - a}{c - a}.$$

As this formula was developed for a very heterogeneous situation with a large number of species, it was desirable to try the formula on a simple association of a relatively small number of species. For this purpose, Smith's Bog, Cheboygan County, Michigan, a *Carex lasiocarpa* stage in bog development, offered itself as an example.

Looking at the bog from the upland surrounding it, the general appearance is that of a mat of almost pure *Carex lasiocarpa* with a small pond near the center. The *Carex* mat covers an area of over 23,000 square meters, or about five acres. Surrounding this mat on the northern, western, and eastern sides are representatives of the high-bog-shrub association in which *Salix pedicellaris* is most abundant. A lowland forest occupies a slight depression at the southern end.

In applying the formula, lines wholly within the obvious *Carex* association were definitely located. Contiguous quadrats one square meter in size were taken on each side of these lines, totalling 1050 quadrats.

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\* A contribution from the Biological Station of the University of Michigan, in which the authors were students under Professor F. C. Gates.

† Gleason, H. A. Species and area. *Ecology* 6: No. 1. 1925.

A plane table map was made of the bog and the limits of the *Carex lasiocarpa* association, from which the area of the association was calculated.

TABLE OF SPECIES FOUND IN QUADRATS AND THE NUMBER OF QUADRATS IN WHICH EACH OCCURRED WITH THE FREQUENCY INDICES CALCULATED.

	Quadrats	F.I.
1. <i>Carex lasiocarpa</i> . . . . .	1050	100
2. <i>Dulichium arundinaceum</i> . . . . .	390	37.1
3. <i>Eleocharis palustris</i> . . . . .	380	36.2
4. <i>Potamogeton heterophyllus</i> . . . . .	240	22.8
5. <i>Eleocharis acuminata</i> . . . . .	207	19.7
6. <i>Juncus canadensis</i> . . . . .	135	12.9
7. <i>Carex crinita</i> . . . . .	94	8.9
8. <i>Lysimachia terrestris</i> . . . . .	61	5.8
9. <i>Potentilla palustris</i> . . . . .	51	4.9
10. <i>Chamaedaphne calyculata</i> . . . . .	50	4.8
11. <i>Hypericum virginicum</i> . . . . .	36	3.4
12. <i>Nymphaea advena</i> . . . . .	28	2.7
13. <i>Carex stricta</i> . . . . .	27	2.6
14. <i>Eriophorum viridicarina</i> . . . . .	14	1.3
15. <i>Panicularia borealis</i> . . . . .	9	0.9
16. <i>Calamagrostis canadensis</i> . . . . .	9	0.9
17. <i>Menyanthes trifoliata</i> . . . . .	2	0.2
18. <i>Carex sterilis</i> . . . . .	1	0.1
19. <i>Salix pedicellaris</i> . . . . .	1	0.1
20. <i>Salix sericea</i> . . . . .	1	0.1
21. <i>Sparganium minimum</i> . . . . .	1	0.1

The average number of species in the 1050 quadrats was 2.65. In addition to the species found in the quadrats taken in the *Carex* mat, the following species of higher plants were found on the mat:

*Andromeda glaucophylla*,      *Lysimachia thyrsiflora*,  
*Eriophorum callithrix*,      *Polygonum amphibium*,  
*Iris versicolor*,      *Scirpus atrocinctus*, and  
*Juncus brachycarpus*,      *Typha latifolia*,

making a total of 29 species on the mat.

Returning to the formula:

$$\frac{\log B - \log A}{\log C - \log A} = \frac{b - a}{c - a},$$

the values obtained in the investigation were as follows:

$$A = 1 \text{ square meter} \qquad a = 2.65$$

$$B = 1050 \text{ square meters} \qquad b = 21$$

$$C = 23,159 \text{ square meters} \qquad c = 29$$

Substituting all but  $c$  in the formula gives:

$$\frac{\log 1050 - \log 1}{\log 23,159 - \log 1} = \frac{21 - 2.65}{c - 2.65}.$$

Solving for  $c$ , we find  $c = 29.16$ . Since the actual number of species is 29, the error between the real and the expected number is 0.55%.

The results of the calculations show that the formula may be applied to a given area in which an association predominates, whether large, as in the aspens, or small, as in the present case. The results also show that the total number of species within the area and not merely those belonging to the association itself must be considered.

#### SUMMARY

1. Efforts have been made to find a mathematical expression for the number of species in a given area.
2. The expression formulated by Gleason:

$$\frac{\log B - \log A}{\log C - \log A} = \frac{b - a}{c - a},$$

in which  $A$  is the area of one quadrat,  $B$  is the area of total quadrats,  $C$  is the area under consideration,  $a$  is the average number of species per quadrat,  $b$  is the total number of species in the quadrats, and  $c$  is the total number of species in the area, had been shown to apply to an association of a large number of species, as the aspen association, but it is now found to apply also to an association of a small number of species, as exemplified by the *Carex lasiocarpa* association at Smith's Bog, Cheboygan County, Michigan.

3. The formula applies to the total number of species present in an area of an association whether they properly belong to the association in question or not.

# INDEX TO AMERICAN BOTANICAL LITERATURE

1924

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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Experiments with various plants to produce change of sex in the individual\*

JOHN H. SCHAFFNER

The writer has had a number of plants under observation and has been experimenting with others which have shown behaviors that tend to throw further light on the problem of the nature of sexuality. It is probable that the problem of sex can only be solved by the accumulation of data from many sources which when finally put together may give such evidence as will lead to the ultimate cause and nature of the remarkable sexual dimorphism exhibited by most living things.

THALICTRUM DIOICUM L.

In the spring of 1921, ten pure carpellate and ten pure staminate plants were dug up and planted in ordinary soil in shallow benches in the greenhouse, thus taking them out of their periodic environment of heat and cold and seasons of moisture and dryness. They were given little attention, except to keep conditions as unfavorable as possible without causing death. Most of these plants bloomed several times during the fall and winter of 1921-22 and also in 1922-23. No change in sex was noted but in the meantime nearly all became decrepit and began to die. By December 1923, only three carpellate plants were still alive and all the staminate had died. One of the survivors developed a small inflorescence which was examined December 3. It contained nine stamens distributed in various, otherwise carpellate flowers. One of the flowers, however, had two stamens. The

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\* Papers from the Department of Botany, The Ohio State University, no. 154.

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stamens were of varying degrees of perfection. Some had pollen sacs with pollen, but apparently none had perfect pollen. In this decidedly dioecious perennial species, therefore, it required more than two years to induce a change in the sexual condition of the individual, but, nevertheless, one carpellate plant out of ten which had passed through a number of reproductive periods in a purely female condition reversed this condition in nine of its sporophylls so that male characters developed. Evidently the originally determined female state was of a very intense and persistent character, and was only gradually overcome by the decided change in its metabolic processes under the unusual adverse environment. This plant and the other two surviving individuals died, with no further development of flowers, in the winter of 1924. The conditions should have been kept a little more favorable for growth.

In the spring of 1922, a carpellate plant which showed some stamens was transplanted from the woods to a pot in the greenhouse and well fertilized with cow manure. The behavior of this plant was reported in 1923 in "Observations on the Sexual State of Various Plants"\* and its record up to date is as follows: In September 1922, the plant bloomed again, producing 14 stamens: one flower having three stamens, some two, and some one. In November of the same year, it bloomed, again with a few stamens. In January 1923, it bloomed once more and this time only carpellate flowers were produced, thus showing a pure female state. The intermediate, bisporangiate, or intersex condition had been changed to a pure female state. By the end of March it was again in anthesis with only pure carpellate flowers. In the meantime the plant was kept richly supplied with manure and water. At the next blooming period, May 11, 1924, the plant was still pure carpellate and the same condition was continued when it bloomed again on June 15 and also on July 20. The plant was neglected during August, but on September 8 it was coming into bloom with a considerable number of flowers, this time producing, among the pure carpellate flowers, four intermediate flowers, each with a single, imperfect stamen. The next blooming period showed a small inflorescence, on November 25, 1924, with all the flowers pure carpellate.

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\* Schaffner, John H. Ohio Jour. Sci. 23: 155.

It is evident, therefore, that labeling a *Thalictrum dioicum* individual at any blooming period as being a pure male or a pure female and thinking to find it so at a future date is a waste of energy, especially if there is very much possibility of change in its environment. Yet, in spite of the fact that occasionally one can find an individual of this species with practically all the flowers bisporangiate, there seems to be a fixedness about the monosporangiate condition which is not easily overcome. This condition, whatever it may be, seems to be the same as that which is developed in the gametophytes of all higher plants, where the given sexual state is handed over from the sporophyte without change and without in the least being disturbed by the reduction divisions. The sex of the gametophyte is but rarely reversed or changed from the state predetermined for it in the sporophyte. Such sporophytes as those of *Thalictrum dioicum*, with strongly fixed sexual states are, therefore, in marked contrast to those of *Thalictrum dasycarpum* F. & L., *Arisaema triphyllum* (L.) Nutt., and *Arisaema dracontium* (L.) Schott, where the sexual condition is so lightly established in the individual that its partial or complete reversal is a comparatively easy matter. Incidentally, the fact must not be overlooked that the intermediate plant described above with a single, vernal blooming period in its normal habitat, under the imposed conditions, actually bloomed five separate times in 1924, strung along from May 11 to November 25. Those who have a wooden notion about the hereditary nature of such ecological or physiological characters will need to re-examine the foundation on which they are standing.

#### CANNABIS SATIVA L.

During the spring of 1924, an unusually interesting case of sex reversal occurred in connection with some rejuvenation experiments, in a carpellate hemp plant. Some hemp seed was planted on January 16, 1924, and, as the result of developing in the short-light period of winter, came into bloom in a little over a month, the staminate first and the carpellate somewhat later. When the carpellate plants were beginning to show their age, but before sex reversal had appeared in very many of them, they were rejuvenated, beginning March 21, by receiving at night, in addition to the available daylight, the light from two 110-watt mazda

electric bulbs. The special individual under consideration was at this time 10 inches high, was pure carpellate, and was producing seed. The tip of the plant was too senile to undergo rejuvenation, but six branches developed from the lower part and began a vigorous growth, showing the usual series of leaf forms that appear in the seedling or in a rejuvenated stem. One of the most vigorous shoots, when it was about 6 inches long, began to bloom and produced twelve flowers. These flowers were all pure staminate and because of the favorable light were all perfectly typical in character, exactly like the summer flowers of pure staminate plants! There was not a vestige of femaleness about them. Because of the continuous light, which should have kept them from blooming in the first place, the plant was soon thrown back completely into the vegetative condition again. On June 5, the electric light was turned off and the rejuvenated plant grew to be large and vigorous, some of the branches being 6 feet tall. On September 8, on returning from a trip to Kansas, the entire plant, including the large branch that had produced the staminate flowers, was in full bloom and all the flowers were pure carpellate again. On September 9, the plant, because of inconvenient size, was severely pruned and rejuvenated again by means of continuous light, daylight in the daytime and electric light at night. As discovered later, this pruning was improperly done, and resulted in the final death of the entire plant. By September 20, numerous buds were developing which later made a good growth. These shoots were so numerous that many were removed and the plant then took on a more vigorous growth. The electric light was discontinued on December 1, and by December 13 the plant began to die. It had, however, produced a considerable number of incipient flowers, an examination of which showed well-developed stigmas. At this fourth blooming period the plant was apparently again pure carpellate, but if death had not cut the blooming period short, it might still have developed some sex reversal, as was rather to be expected for the season of the year. It is now clear to the writer, from this and other experiments, that hemp will endure considerable pruning and cutting back of the active growing tops, but if the entire plant is cut off at or below the part still bearing leaves, or if any large branches are removed, death is almost sure to follow, the destruction gradually passing down the stem until the tissue is reached that is supporting the growing branches.

Here was a carpellate plant, originally pure female in both vegetative and reproductive expression, which developed in a later reproductive period a pure male expression, and at a still later period pure female expression again. The cell lineage, which was originally in the female state, showed reversal to maleness and then re-reversal to femaleness again. These reversals in zones of growth are similar to the zonal successions and reversals shown by many monoecious plants, with this important difference, however. While a monoecious plant has a neutral vegetative growth and the first sexual state appears in this neutral tissue, the carpellate hemp plant was, as its vegetative character showed, at first in the female state, from the time of the embryonic development until it was rejuvenated. The behavior of this carpellate plant suggests some definite methods of procedure to produce similar results. No flowers should have appeared during the vigorous vegetative growth after rejuvenation and the continuous light should also check sex reversal under normal conditions. Now the writer has shown that in experiments on sex reversal of carpellate hemp plants, a considerable number of individuals show no reversal to maleness until they are becoming very senile, often not until it finally occurs in branches coming from very decrepit stems. In general, the tendency in both staminate and carpellate plants under short light conditions is toward maleness. Staminate plants usually show reversal to femaleness most decidedly at the very beginning of the blooming period, while carpellate plants, as stated, often show no reversal to maleness until extreme old age. In the ordinary annual development there appears to be an up and down gradient, and it is on the down grade of functional activity toward a low functional condition that with a suitable environment a proper state develops for reversal to maleness. Now assuming that the given plant was in a very low vegetative condition and a very decrepit state of senility, as it actually appeared to be at the first rejuvenation, the rejuvenation process would begin a reverse gradient of physiological states becoming more and more normal, and the condition would be passed through in which hereditary factors of anthesis become active, but the senile or other condition which precedes the development of a male state was also attained at this point, in the up grade toward a normal vegetative condition, so the plant not only bloomed but was

thrown completely into a typical male expression, which lasted until the normal vegetative state was attained again. A method should, therefore, be possible by which this same result could be duplicated at will in a certain percentage of cases.

Another point, which presents itself to the writer in an example like the present one, is that such cases of re-reversal answer fully the contention of some who are inclined to interpret simple reversals as cases of abnormal chromosome or factor shiftings or displacements. Such explanations are not only contrary to the evidence in simple reversals, but become ridiculous in the case of double reversals. In view of the fact that exactly similar back and forth reversals take place in many known cases, as for instance in the diploid, parthenogenetic cycle of *Leontodon*, reported by Sears\* and others, and in the haploid, parthenogenetic cycle of *Datura*, as reported by Blakeslee and Belling,† it seems to the writer that any supposition except a physiological basis for sexuality is entirely unreasonable.

McPhee‡ obtained complete sex reversal in two staminate plants which were apparently pure staminate at first and later in their lives produced nothing but carpellate flowers and matured seeds. Such cases might give interesting results with several successive rejuvenations. The writer has noted such individual deviations from the more typical behavior of femaleness to maleness and in his "Sex Reversal in the Japanese Hop" said that "In hemp the general tendency appears in age to be towards maleness in both staminate and carpellate plants, although some individuals are exceptional in this respect."§ McPhee obtained in general much lower percentages of reversal than the writer, which may have been due to a number of causes, as not keeping the plants alive long enough, too poor soil, etc.

McPhee apparently has a rather confused notion of what constitutes "sex reversal," a confusion probably arising from reasoning from determinate higher animals with a single develop-

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\* Sears, Paul B. Amiotic parthenogenesis in *Taraxacum vulgare* (Lam.) Schrk. and *Taraxacum laevigatum* (Willd.) DC. Ohio Jour. Sci. 17: 97-100. 1917.

† Blakeslee, Albert F., and Belling, John. Chromosomal mutations in the Jimson weed, *Datura stramonium*. Jour. Hered. 15: 195-206. 1924.

‡ McPhee, Hugh C. The influence of environment on sex in hemp, *Cannabis sativa* L. Jour. Agr. Res. 28: 1067-1080. 1924.

§ Bull. Torrey Club. 50: 75. 1923.

mental period. The sex reversal is genetically and physiologically the same whether it is accomplished in the plumule and continues for an indefinite period (which would then be a "true" sex reversal according to McPhee, because no intersexuality would be present) or whether it takes place in a single flower-bud or in a single sporophyll (which would not be sex reversal according to McPhee). If we are to discuss the intricate problem of sexuality in plants intelligently, we evidently need to have some considerable knowledge of the morphology, physiology, and general nature of plants.

McPhee has not at all given a correct notion of the evidence published by the writer when he says: "It is true that Schaffner has obtained as high as 88 per cent of "sex reversal" in one plat which was grown in the greenhouse during the short days of winter, but when we consider that the plat contained only 16 plants, we must be careful in drawing the conclusion that the same percentage of plants in a much larger plat would show the same change." How any one could get such a notion from my two main papers on hemp cited by McPhee is beyond comprehension! In plain tables among other high records are the following:

Plat 1,	18	carpellate plants—reversed	16.
Plat 2,	36	carpellate plants—reversed	32.
Plat 3,	29	carpellate plants—reversed	25.
Plat 4,	116	staminate plants—reversed	104.
Plat 5,	66	staminate plants—reversed	62.
Plat 6,	42	staminate plants—reversed	39.
Plat 7,	30	staminate plants—reversed	27.

So there is plenty of evidence to show that the writer's conclusion was correct that one could predict 90% or more of sex-reversal by employing the proper methods. It is so simple and easy that one with the merest knowledge of how to grow plants can do it.

#### MORUS ALBA L.

A number of years ago the writer reported a very striking case of sex reversal in the white mulberry.\* A staminate tree had reversed a large branch to a partly female condition, so that

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\* Schaffner, John H. The nature of the diecious condition in *Morus alba* and *Salix amygdaloides*. Ohio Jour. Sci. 19: 409-416. 1919.

the branch in question produced not only carpellate catkins and catkins partly carpellate and partly staminate, but also continued to produce pure staminate catkins commingled with the other two types. Although no self-pollination was attempted, it is probable, from the fact that no staminate trees were near this special individual, that the abundant fruit produced was largely self-pollinated. However this may have been, the seed produced was plainly the offspring of two originally staminate parents. A considerable number of seedlings were grown, twelve of which were saved and planted in the garden near the botanical greenhouse on the Ohio State University Campus. Ten of these trees survived and developed to maturity. In the spring of their first blooming period, 1922, a severe frost occurred when the flowers were beginning to expand, which destroyed the entire crop and no study could therefore be made of the sexual conditions of the plants. In 1923, all the ten surviving trees bloomed and were studied in detail. There were seven carpellate individuals and three staminate individuals, and all appeared pure as to sex in the early part of the blooming period. But continued studies showed that toward the end of the blooming period some individuals were intermediate in sexual expression. Two carpellate plants each developed a partial staminate condition. On one catkin there was a staminate flower with four pollen-shedding stamens and some unopened stamens at the base of the catkin. The tip of the catkin was normally carpellate. The other tree also showed a number of staminate flowers more or less perfect in condition. One of the staminate trees produced two catkins with a slight development of femaleness, having enlarged ovaries and reduced stamens. These catkins showed the usual carpellate character in the tardiness of the development of the abscission layers. In 1924, all of the ten trees bloomed again, the seven carpellate individuals being all pure carpellate and the three staminate individuals all pure staminate. No reversal whatever was found, although the plants were studied very carefully.

This experiment, so far as it goes, shows that Yampolsky's\* finding for *Mercurialis annua*, where reversed, self-pollinated staminate individuals tended to reproduce maleness, and re-

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\* Yampolsky, Cecil. Inheritance of sex in *Mercurialis annua*. Am. Jour. Bot. 6: 410-442. 1919.

versed, selfed carpellate individuals, tended to reproduce femaleness in their offspring, may be only a special case and not of general application. For, as stated, of the ten seedlings from the originally staminate mother parent, seven were female in expression. It is probable that in many cases Yampolsky's findings would hold, for it appears that the original sex condition of the individual which has reversed the special branches or flowers should be more readily established again in the parasitic embryos and that this condition would tend to be continued or intensified up to maturity. But if sex is not primarily determined by specific hereditary factors we would expect the rule to work one way about as often as the other. But my material is too incomplete for speculation. In the spring of 1924, a staminate tree near the Botany-Zoology building of the Ohio State University showed signs of sex reversal on several small branches. Two of these branches were promptly covered with cloth with some staminate catkins included to insure self-pollination. Several self-pollinated fruits were thus obtained, from which 55 seedlings sprouted and are at present growing well in the botanical greenhouse. In several years, therefore, a good number of these plants should be available for study, and settle definitely the problem in so far as the male condition is concerned. To obtain selfed seed from carpellate plants will not be so easy, since usually by the time staminate reversals are discovered, pollination from outside sources may already have taken place. Nevertheless, there are often very isolated trees in country districts, and where such are known, selfed seed should be readily obtained if proper precautions are taken. The writer has known such trees, but never in places available to him for study at the proper time. Any one who is in a position to obtain selfed seed from a carpellate white mulberry should by all means do so.

The question arises as to the possible parthenogenetic development of the white mulberry. But in view of the fact that Tahara\* found 14 haploid and 28 diploid chromosomes in *Morus indica* L. and also 28 diploid chromosomes in *M. alba*, the life cycle is probably normal. Nevertheless it would be desirable to have the gametophytic number definitely established. If this has been done it is not known to the writer. Triploid mu-

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\* Tahara, Masato. Ueber die Kernteilung bei *Morus*. Bot. Mag. Tokyo 24: 281-289. 1910.



tants are known to occur. But on the other hand, if the white mulberry were parthenogenetic through diploid eggs, the results obtained would still show that each sex does not tend to reproduce itself in this species.

In any event, the white mulberry is able to reproduce offspring of both sexual states from individuals which were originally male. Apparently the seven carpellate and three staminate plants were produced from the union of two cells derived from two individuals that were originally in the male state. Crew\* has reported the production of two chickens, one a male and the other a female, from two parents which were both originally hens, but one of which reversed its sex because of a diseased condition.

#### ARISAEMA TRIPHYLLUM (L.) Torr.

The writer† published a paper in February 1922 on the control of sex in Jack-in-the-pulpit, and since the experiments were continued for two years after the first report, the results for these two years are herewith presented to complete the record. As reported in the previous paper, 25 pure carpellate plants, five intermediate plants and ten pure staminate plants were dug up and transplanted to the north side of the botanical greenhouse. They were treated for maleness and the next spring, 1920, the nine surviving staminate plants were still pure staminate, the five intermediate or monoecious plants were all pure staminate, and of the 25 originally pure carpellate plants, 21 were now pure staminate, two were intermediate, and two remained pure carpellate. They were immediately treated for reversal to femaleness and in the spring of 1921 came up as follows: The nine originally staminate plants were all pure carpellate except one individual which had three staminate flowers at the tip of its inflorescence. Of the five originally intermediate plants, four were pure carpellate and one which had branched gave rise to two staminate shoots. Of the 25 originally pure carpellate plants, one failed to bloom, one was pure staminate, one was intermediate carpellate

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\* Crew, F. A. E. Complete sex-transformation in the domestic fowl. Jour. Hered. 14: 361-362. 1923.

† Schaffner, John H. Control of the sexual state in *Arisaema triphyllum* and *Arisaema dracontium*. Am. Jour. Bot. 9: 72-78.

with a single staminate flower at the tip of the inflorescence, and 22 were pure carpellate again.

In 1922, the plants having been treated for maleness, the control was as follows: Of the ten originally staminate plants six bloomed and all were pure staminate. Of the five originally intermediate plants, now increased to six, three bloomed, of which one was pure staminate, one was intermediate with only eight carpellate flowers at the base, and one was intermediate with a greater number of carpellate flowers than staminate ones. Of the 25 originally carpellate plants, one had twinned, both of which bloomed along with seven others. Of these nine plants, the twins and six others were pure staminate and one was intermediate with more carpellate flowers than staminate ones.

The plants were immediately treated again for femaleness and in the spring of 1923 the results were as follows: Of the ten originally staminate plants, one of which had died, eight bloomed; seven were pure carpellate and one was nearly pure carpellate, having a single imperfect staminate flower at the tip. Only three of the numerous shoots which were appearing in the patch bloomed and two of them were staminate and one intermediate but with mostly staminate flowers. These small plants, offshoots from the original corms, developed maleness in spite of the fact that the treatment given reversed all of the large mature corms. This was probably due to the small size of the offshoots and consequent lack of food supply, the leaf surface being, naturally, very small the previous year. Apparently most if not all small offshoots are at first staminate under ordinary conditions. Of the five originally intermediate plants, previously increased to six, four bloomed, all pure female. Of the 25 originally pure carpellate plants changed to 26, through one twinning by dichotomous branching, 13 bloomed, of which ten were pure carpellate, one was carpellate except that it had a single imperfect staminate flower at the tip of the inflorescence, one was intermediate, and one was pure staminate probably because of a reduction of its corm by branching. From the 25 originally pure carpellate plants, numerous offshoots had also appeared the two past years and of these seven came into bloom. There were five pure staminate plants, one staminate with a single carpellate flower at the base of the spadix, and one intermediate, but with more staminate flowers than carpellate ones. Thus, as in the

case of the offshoots from the originally staminate plants, the small offshoots from the originally carpellate plants were at first also staminate or nearly staminate in spite of the fact that the treatment given the previous year to induce femaleness produced the proper effect in the mature plants with large corms and large leaf surfaces.

It is evident that the control for the last two years was as perfect as for the first two years in all cases where the plant had not been decidedly reduced by vegetative propagation. In experimenting on sex control with *Arisaema triphyllum*, therefore, the process should not be continued beyond three or four years, unless special means are used to prevent any considerable amount of vegetative multiplication.

#### ARISAEMA DRACONTIUM (L.) Schott

Two records were also obtained in the summer of 1922 for the green-dragon. Two staminate plants which had been treated for femaleness changed to typical monoecious individuals. Monoecious plants had also been treated at the same time for maleness, but only two came out of the ground and neither bloomed. The treatment was too extreme. But the evidence shows again that *Arisaema dracontium*, as stated in my 1922 paper, changes from the staminate to the monoecious condition. With the cases previously reported, it is plain that *Arisaema dracontium* can be thrown from monoeciousness to pure staminateness and from pure staminateness to monoeciousness. It is probable that with a little experience this could be done as easily as the sexual condition can be changed in *Arisaema triphyllum*.

It is interesting to remember that *Arisaema* is at the top of one of the main lines of phyletic evolution in the Aroids. It is not only high in the scale of morphological advancement, but is the only genus that contains dioecious species. The lowest Aroids have bisporangiate flowers, the great mass of higher Aroids are monoecious, and *Arisaema* has advanced just far enough into the dioecious stage to show still monoecious conditions, as in *Arisaema dracontium*. A correct taxonomy and phylogeny will do much to help us to a correct understanding of the fundamental properties and possibilities of a species.

## SUMMARY

1. *Thalictrum dioicum* was changed from a pure carpellate condition to an intermediate condition, showing maleness. Intermediate plants have also been changed to a pure carpellate condition and then back again to the original condition. These conditions, therefore, do not represent fixed, hereditary constitutions.

2. A pure carpellate *Cannabis sativa* plant has been rejuvenated and changed to a pure male expression and then back again to a pure female expression. Thus a cell lineage can change from one sexual state to the other and back again without any change in chromosome complement or hereditary constitution.

3. In *Morus alba*, offspring from seed produced on a reversed branch of a staminate plant did not tend to repeat maleness, but of ten individuals raised to maturity, seven were carpellate and three staminate.

4. Continuation of the experiments on *Arisaema triphyllum* show a nearly perfect control of the sex of the individual for the third and fourth years of the experiment. They also show that the small offshoots, whether they come from plants which are for the time being either carpellate or staminate and whether they have been treated for femaleness or maleness, are probably nearly always in the male condition at their first blooming period.

5. In 1922, two staminate plants of *Arisaema dracontium* were changed to typical monoecious individuals, adding to the record of definitely induced sex reversal in this species.

6. All of these experiments add decidedly to the weight of the accumulating evidence that sexuality is primarily a physiological condition, that it is primarily not at all Mendelian in nature and not amenable to Mendelian analysis; that it can frequently be controlled and reversed at will, even with our present crude methods, and that it is preeminently a subject for ecological and physiological experimentation.

7. A final conclusion is that the time has arrived for an honest revision of the ordinary textbooks and treatises dealing with heredity and sex, to conform them to the evidence established, and to discontinue the presentation of untenable hypotheses, which in the first place had little more evidence in fact as a basis for their promulgation than the fertile imagination of their proponents.

COLUMBUS, OHIO



## Studies on the flora of northern South America—III

H. A. GLEASON

(WITH PLATE 3)

### NEW OR NOTEWORTHY SPECIES OF CENTROPOGON AND SIPHOCAMPYLUS

The genus *Centropogon*, so abundantly represented in the Andean region of northwestern South America, may be conveniently divided into three groups, based largely on superficial characters and not always indicative of true relationships among the species. One of these, characterized by the presence of branched hairs resembling those of *Verbascum*, has been discussed in the preceding number of this series. A second is characterized by the crowding of the flowers into a dense terminal cluster or raceme, while the third has axillary flowers subtended by normal foliage leaves. The second of these may in turn be divided into two portions, the one with large leaves, a crowded inflorescence, and erect sepals, commonly represented in herbaria by *C. speciosus* Planch., *C. Planchonis* Zahlbr., and the Central American *C. nutans* Planch. & Oerst., and aptly called section *Amplifolii* by Zahlbruckner; the other with small leaves, an elongate inflorescence, and reflexed sepals, best illustrated in American herbaria by the Bolivian *C. yungasensis* Britton. The third group is still more easily susceptible of division into a portion with penicillate anthers and another with appendiculate anthers, of which the widely distributed *C. cornutus* (L.) Druce (*C. surinamensis* L.) is the best known example.

### CENTROPOGON, GROUP AMPLIFOLII

This easily recognized group of species, distinguished first by Zahlbruckner, is characterized chiefly by the inflorescence, which consists of an abbreviated, bracted raceme, in which the flowers are borne on short peduncles. The anther-appendage consists of concrescent hairs, producing a stiff, erect or reflexed, triangular scale; the leaves are large and thin and frequently broadest above the middle; the sepals are erect or appressed; the corollas are red; the pubescence, if any, is thin, and consists of straight or barely crooked short hairs. There is usually a sharp distinction in

size between the uppermost foliage leaf and the lowest bract, and the raceme is in some species conspicuously elevated above the uppermost leaf. In a few species, the raceme tends to elongate after flowering, or continues to bear crowded flowers at the end, while the lower, fruiting portion is elongated. In such cases, the members of the *Amplifolii* may bear a superficial resemblance to the related group *Axillares*, containing, among others, the well-known *C. cornutus* (L.) Druce. The group is also closely related to *C. yungasensis* Britton and its allies, which also have a terminal raceme, usually more elongate, however, and in which the sepals are distinctly spreading or reflexed. Thirty-five species of *Centropogon* have been described with these characters and probably belong to this group. Those known to me from South America, including several additional species, may be distinguished as follows:

- A. Sepals contiguous or united at base, the sinuses therefore narrow and acute; anther-appendage without a basal zone of separate hairs.
  - I. Calyx strongly gamosepalous.
    - Calyx-lobes broadly ovate, prominently dentate. . . . . 1. *C. roseus*
    - Calyx-lobes triangular-lanceolate.
      - Anther-tube densely hirsute . . . . . 2. *C. gamosepalus*
      - Anther-tube essentially glabrous . . . . . 3. *C. capitatus*
  - II. Sepals separate, or barely united at their bases.
    - Sepals 4-5 mm. long, about equaling the hypanthium; leaves ample, obovate, abruptly apiculate . . . . . 4. *C. grandis*
    - Sepals 6-12 mm. long, much exceeding the hypanthium.
      - Calyx and corolla glabrous or essentially so.
        - Sepals 5-6 mm. long, 3 mm. wide . . . . . 5. *C. Bangi*
        - Sepals 10 mm. long, 2 mm. wide . . . . . 6. *C. amplifolius*
      - Calyx and corolla distinctly hirtellous.
        - Leaves closely puberulent on the veins beneath with very short brown hairs; sepals prominently veined . . . . . 7. *C. congestus*
        - Leaves hirsute beneath on the veins, and frequently also on the surface.
          - Corolla about 30 mm. long.
            - Leaves elliptic to obovate-oblong, broad.
              - Sepals 16 mm. long; anthers pilose. . . . . 8. *C. gesnerioides*
              - Sepals 4-5 mm. long; anthers glabrous . . . . . 9. *C. gesneraeformis*
            - Leaves narrowly lance-oblong, about 6 times as long as wide . . . . . 10. *C. angustus*

- Corolla about 45 mm. long. . . . . 11. *C. serratus*
- B. Sepals separated by broad, flat or rounded sinuses;  
anther-appendage (except in one species) with  
a distinct basal zone of hairs.
- Sepals 1-4 mm. long, shorter than the hypanthium.  
Leaves conspicuously long-acuminate at base.
- Corolla stout, 12 mm. wide at the throat  
when pressed; sepals ovate, 2 mm. long. . . . 12. *C. curvatus*
- Corolla slender, less than 10 mm. wide at the  
throat when pressed.
- Calyx glabrous; sepals appressed. . . . . 13. *C. parvulus*
- Calyx hirtellous; sepals recurved at the  
extreme tip. . . . . 14. *C. arcuatus*
- Leaves rounded to broadly acute at base. . . . 15. *C. cuspidatus*
- Sepals 9-12 mm. long.
- Leaves obtuse, softly pubescent beneath. . . . 16. *C. beslerioides*
- Leaves acute or acuminate, glabrous beneath.
- Leaves minutely callous-denticulate; bracts  
obtuse, entire. . . . . 17. *C. pedicellaris*
- Leaves finely ciliate, denticulate; bracts acute,  
denticulate. . . . . 18. *C. ciliatus*
- Sepals 5-7 mm. long.
- Corolla-tube abruptly bent, nearly or quite at  
right angles. . . . . 19. *C. aggregatus*
- Corolla-tube straight or curved, but never  
approaching a right angle.
- Leaves obovate-oblong, broadest well above  
the middle, long-cuneate at base. . . . . 20. *C. speciosus*
- Leaves oblong, broadest at or below the  
middle.
- Leaves softly pubescent beneath. . . . . 21. *C. albolimbatus*
- Leaves glabrous beneath.
- Leaves broadly rounded at base. . . . . 22. *C. prostratus*
- Leaves acute at the base.
- Anther-tube glabrous or essentially so. . . . 23. *C. solanifolius*
- Anther-tube hirsute on the dorsal side  
with violet hairs. . . . . 24. *C. Planchonis*

1. CENTROPOGON ROSEUS Rusby, Bull. N. Y. Bot.  
Gard. 8: 123. 1912.

Bolivia: Tumupasa, Dept. La Paz, alt. 1800 ft., *Williams* 584  
(type, herb. N. Y. Botanical Garden) 10 Jan. 1902.

2. CENTROPOGON GAMOSEPALUS Zahlbr. Ann.  
Naturh. Hofmus. Wien 6: 434. 1891.

Peru: Tarapoto, Dept. Loreto, *Spruce* 4131 (type, herb. Kew).



3. *CENTROPOGON CAPITATUS* Drake, Jour. de Bot. 3:  
238. 1889.

Ecuador: Huacapamba, near Loja, *Poortman* 198 (type, herb. Mus. Paris). Peru: Tarapoto, *Spruce* 4132.

4. *CENTROPOGON GRANDIS* (L.f.) Presl, Prod.  
Monog. Lobel. 48. 1836.

*Lobelia grandis* L.f. Suppl. 394. 1781.

*Siphocampylus grandis* G. Don, Gen. Syst. 3: 702. 1834.

Colombia: near Bogota, alt. 2560 m., *Bonpland* (herb. Mus Paris); Tequendama, Dept. Cundinamarca, alt. 2400 m., *Pennell* 1960, 15 Sept. 1917; Salento, Dept. Caldas, alt. 2100-2500 m., *Pennell* 8866, 25-31 July 1922.

5. *CENTROPOGON BANGI* Zahlbr. Bull. Torrey Club 24:  
372. 1897.

Bolivia: Yungas, forest region northeast of La Paz, alt. 4000 ft., *Bang* 500 (type); *Rusby* 1093, 1885.

6. *CENTROPOGON AMPLIFOLIUS* Vatke, Linnaea 38: 716.  
1874.

Bolivia: Santa Rosa, *Kuntze*. Peru: La Merced, Dept. Junin, alt. about 4000 ft., *Macbride* 5662, 27 Aug.-1 Sept. 1923.

7. *Centropogon congestus* n. sp. Stem herbaceous, strongly angled or grooved and somewhat flattened above, thinly puberulent when young, glabrous in age, the internodes 3-4 cm. long; leaf-blades thin and membranous, oblong to oblong-obovate, 15-28 cm. long, 6-10 cm. wide, abruptly short-acuminate, sharply serrulate (about 6 teeth per cm. of margin, 0.5 mm. high), each tooth with an oblong, intramarginal callosity, acuminate at the base into an indefinite petiole 1-3 cm. long, above glabrous on the surface, minutely puberulent on the midvein, beneath minutely puberulent, thinly on the surface, densely on the principal veins; lateral veins about 1 cm. apart, diverging at nearly right angles and arcuately ascending; inflorescence a terminal crowded raceme, at length elongate; floral leaves oblong to oblanceolate, 2-3 cm. long, sharply acute, cuneate at base, pubescent like the foliage leaves; pedicels 2-3 cm. long, slender, sparsely pubescent; hypanthium urceolate-hemispheric, 5 mm. high, 8 mm. wide when pressed, sparsely puberulent; sepals narrowly triangular, 10 mm. long, 3 mm. wide at base, about

7-ribbed, reticulate-veined, minutely puberulent, separated by acute sinuses, or gamosepalous for 1 mm. at the base; corolla red, sparsely puberulent, 30 mm. long, the tube prominently decurved, 23 mm. long, the lobes triangular-falcate, acuminate, prominently deflexed; filaments glabrous, exerted 5-7 mm.; anther-tube pubescent, especially at the base, the two lower anthers with a cartilaginous appendix. FIG. 1.

Type, *Pennell 10,169*, collected 30 Aug. 1922 at Pereira, Dept. Caldas, Colombia, altitude 1400-1500 m., and deposited in the herbarium of the New York Botanical Garden. Other collections are *Pennell, Killip & Hazen 8726*, Rio Quindio, above Armenia, Dept. Caldas, alt. 1400-1600 m., 25 July 1922; *Killip & Hazen 8764*, Salento, Dept. Caldas, alt. 1600-1900 m., 27-31 July 1922; *Lehmann 1201*; and *Darwe 804*, Quindio, alt. 2000 m., 1918, in the same herbarium.

8. *Centropogon gesnerioides* n. sp. All parts of the plant subhirsute with straight or slightly curved, flattened, white hairs, tapering regularly from the base to the apex; stem herbaceous or suffruticose, strongly angled above, becoming glabrous with age; leaves obovate-oblong, thin and membranous, the largest 24 cm. long by 8.5 cm. wide, acuminate, minutely denticulate with callous, mainly intramarginal teeth (about 5-7 teeth per cm. of margin, 0.4 mm. high), acuminate at base into an indefinite petiole 2-3 cm. long, thinly pubescent above, more densely beneath, especially along the principal veins; lateral veins about 1 cm. apart, widely divergent and arcuately ascending; inflorescence a terminal raceme, at length elongate; floral leaves oblong, sessile, 2-3 cm. long, densely pubescent; pedicels slender, 2 cm. long; hypanthium urceolate-hemispheric, 4 mm. long, 7 mm. wide when pressed, densely pubescent; sepals triangular, erect or somewhat spreading, 16 mm. long, 5 mm. wide at base, acuminate, sparsely denticulate; corolla red, conspicuously hirsute, especially distally, 30 mm. long, the tube prominently decurved, 25 mm. long, the lobes triangular-falcate, acuminate, deflexed; filaments hirsute, especially toward the summit, exerted 3-4 mm.; anther-tube 7 mm. long, sparsely pilose, the two lower anthers with a cartilaginous appendix. FIG. 2.

Type, *Pitier 691*, collected Dec. 1905, Cuestá de Tocotá, road from Buenaventura to Cali, Dept. El Valle, Colombia, altitude 1500-1900 m., and deposited in the United States National Herbarium. The species is sharply differentiated from *C. congestus* Gleason by its larger sepals and hirsute pubescence; from *C. gesneraeformis* Drake by its longer sepals, longer hairs, and hirsute anthers.

9. *C. GESNERAEFORMIS* Drake, Jour. de Bot. 3:  
239. 1889.

Peru: Muña, Dept. Huánuco, alt. about 7000 ft., *Macbride* 3982, 23 May–4 June 1923. Ecuador: Huacapamba, near Loja, *Poortman* 224 (type, herb. Mus. Paris). Colombia: "Balsillas" on Rio Balsillas, Dept. Huila, alt. 2100–2200 m., *Rusby & Pennell* 790, 816, 3–5 Aug. 1917; "La Gallera," Micay Valley, Dept. El Cauca, alt. 1400–1500 m., *Killip* 7700, 29–30 June 1922.

10. *Centropogon angustus* n. sp. Stem herbaceous, 6–12 dm. high, prominently grooved, closely and finely pubescent; leaves thin, membranous, narrowly oblong, 14–17 cm. long, 2.5–3 cm. wide, long-acuminate, prominently and irregularly serrulate (about 6 teeth per cm. of margin, 0.5–1 mm. high), each tooth with a narrow intramarginal callosity, long-cuneate at base into an indefinite petiole 1–2 cm. long, minutely and sparsely puberulent on the surface, densely pubescent on the veins above, sparsely short-hirsute on the veins beneath; lateral veins inconspicuous, 5–8 mm. apart, strongly ascending; inflorescence a crowded terminal raceme, the floral leaves resembling the cauline in form, and pubescence gradually reduced in size from 10 to 2 cm. in length; pedicels slender, finely pubescent, 3 cm. long at anthesis, ultimately elongating to 7 cm.; hypanthium urceolate-hemispheric, 4 mm. long, 7 mm. wide when pressed, thinly pubescent with short, straight, white hairs; sepals erect, narrowly triangular, 11 mm. long, 3.5 mm. wide at the base, acuminate, entire, pubescent like the hypanthium; corolla red, slightly decurved, about 30 mm. long, the tube 22 mm. long, minutely puberulent, the lobes narrowly triangular-falcate, acuminate, deflexed; filaments barely exerted, essentially glabrous; anther-tube 6–7 mm. long, glabrous, the two lower anthers with a cartilaginous appendix. FIG. 3.

Type, *Macbride* 4967, collected 17–26 July 1923, at Vilcabamba, hacienda on Rio Chinchao, Dept. Huánuco, Peru, altitude about 6000 feet, and deposited in the herbarium of The New York Botanical Garden (duplicate in herb. Field Museum). The species is distinguished from all of its relatives, including *C. congestus* Gleason, *C. gesneraeformis* Drake, and *C. gesnerioides* Gleason, by its narrow leaves and sepals, its large floral leaves, and elongate pedicels.

11. *Centropogon serratus* n. sp. Stem shrubby, climbing, densely pubescent or subtomentose above with stout, flattened, crooked, pale brown hairs, glabrescent with age, the internodes 2–4 cm. long; petioles stout, 5–8 mm. long, pubescent like the

stem; leaf-blades thin and membranous, broadly elliptic, 8-9 cm. long, 4.5 cm. wide, obtuse, broadly cuneate and somewhat inequilateral at base, prominently serrate (2-3 teeth per cm. of margin, 1-1.5 mm. high), each tooth with an oblong intramarginal callosity, very sparsely short-hirsute with pale brown hairs above, more prominently so on the surface beneath and densely on the principal veins; lateral veins 8-12 mm. apart, ascending at an angle of  $45^{\circ}$ , veinlets inconspicuously reticulate; inflorescence a crowded terminal raceme; floral leaves obovate, 20-25 mm. long, 12-17 mm. wide, short-petioled, pubescent like the cauline, but more densely; pedicels 2-3 cm. long, pubescent like the stem; hypanthium broadly hemispheric, 5 mm. high, 8 mm. wide when pressed, thinly hirsute with the same type of hairs; sepals erect, narrowly triangular, 6 mm. long, 3 mm. wide at base, densely hirsute, entire, separated by acute sinuses; corolla red, 45 mm. long, thinly pubescent with stout, flattened, white hairs, the tube straight, 40 mm. long, the lobes triangular-falcate, strongly deflexed; filaments barely exerted, glabrous; anther-tube 7 mm. long, purple, sparsely short-hirsute at the apex, the two lower anthers with a cartilaginous appendix. FIG. 4.

Type, *Killip 9759*, collected 14 Aug. 1922, Quebrada Cajamarca to "Mermillon," New Quindio Trail, Dept. Tolima, Colombia, and deposited in the herbarium of The New York Botanical Garden. The species is well characterized by its prominently serrate leaves, its coarse subtomentose pubescence, and its large corollas.

12. *Centropogon curvatus* n. sp. Stem apparently herbaceous, angled, sparsely pubescent above, soon becoming glabrous, the internodes 1-2 cm. long; leaf-blades narrowly elliptic-oblong, thin and membranous, 15-20 cm. long, 3-4, or rarely 5, cm. wide, acuminate, minutely denticulate with barely salient callous teeth (about 2 teeth per cm. of margin, 0.2 mm. high), acuminate at base into an indefinite petiole 12-20 mm. long, glabrous on both sides; lateral veins 15-20 mm. apart, ascending at an angle of  $45^{\circ}$ , the veinlets obscure and reticulate; inflorescence a terminal, few-flowered, subcapitate raceme, the floral leaves 15 mm. long; pedicels pubescent, 8-10 mm. long; hypanthium broadly hemispheric, 3 mm. high, 7 mm. wide when pressed, sparsely and minutely pubescent; sepals erect, appressed, triangular, 2.5 mm. long, 1.5 mm. wide at base, acute, minutely ciliate, separated by broad sinuses; corolla 38 mm. long, minutely puberulent, the tube prominently decurved and 12 mm. wide at the throat, the lobes broadly triangular-falcate, short, acuminate, deflexed; filaments glabrous, becoming pubescent at the summit, exerted 5-8 mm.; anther-tube 9 mm. long, densely

pubescent on the dorsal side with purple hairs, the two lower anthers with a cartilaginous appendix. FIG. 5.

Type, *Rusby & Pennell 948*, collected 1-8 Aug. 1917, east of Neiva, Dept. Huila, Colombia, altitude 1300-1800 m., and deposited in the herbarium of The New York Botanical Garden. The species is distinguished from others of this group with minute sepals by its unusually long and stout corolla.

13. *Centropogon parvulus* n. sp. Stem climbing, faintly striate or somewhat angled above, closely and scabrously pubescent, the internodes 2.5-5 cm. long; petioles stout, puberulent, 4 mm. long; leaf-blades oblong-lanceolate or narrowly oblong-elliptic, 8-12 cm. long, 25-35 mm. wide, acuminate, sharply serrulate (2-3 teeth per cm. of margin, 0.5 mm. high), gradually tapering to an acute base, glabrous above, minutely puberulent on the plane, prominently reticulate veins beneath; inflorescence a crowded terminal raceme, eventually elongate; floral leaves reduced to subulate bracts 4 mm. long; pedicels 15-25 mm. long, minutely bracteolate near the base; hypanthium subglobose, 7 mm. long, 6 mm. wide when pressed, glabrous; sepals appressed, triangular, 3 mm. long, 1 mm. wide at base, glabrous, separated by broad flat sinuses; corolla yellow, red toward the base, strongly decurved, scabrellate, the tube 30 mm. long, the lobes broadly triangular-falcate, strongly deflexed, the upper 10 mm. long; filaments included; anther-tube densely hirsute with pale yellow hairs, the two lower anthers with a cartilaginous appendix. FIG. 6.

Type, *Macbride 4848*, collected 19-23 June 1923, Cushi, Peru, altitude about 5000 feet, and deposited in the herbarium of The New York Botanical Garden (duplicate in herb. Field Museum). Its nearest relative is *C. arcuatus* Wimmer, in which the calyx and corolla are strongly hirtellous and the sepals recurved at the apex.

14. *CENTROPOGON ARCUATUS* Wimmer, Repert.  
Spec. Nov. 19: 242. 1924.

Ecuador: Andes, *Spruce 5375* (duplicate of type in herb. Kew, Gray).

15. *CENTROPOGON CUSPIDATUS* A. DC. Prodr.  
7: 346. 1839.

Peru: La Merced, alt. about 4000 ft., *Macbride 5654*, 27 Aug. -1 Sept. 1923; Pampayacu, alt. 3500 ft., *Macbride 5088*, 19-25 July 1923; *Dombey* (type, herb. Mus. Paris).

16. *CENTROPOGON BESLERIODES* (H.B.K.) A. DC.

Prodr. 7: 346. 1839.

*Lobelia beslerioides* H.B.K., Nov. Gen. & Sp. 3: 306. 1818.

Colombia: Popayan Andes (?), *Bonpland* (type, herb. Mus. Paris); "Pinares" above Salento, Dept. Caldas, alt. 2700-2900 m., *Pennell* 9333, 2-10 Aug. 1922; "Alaska" above Salento, alt. 3100-3400 m., *Pennell*, 9376, 7 Aug. 1922.

17. *Centropogon pedicellaris* n. sp. Stem herbaceous or suffruticose, irregularly striate when dry, glabrous below the inflorescence, the internodes 3-6 cm. long; petioles 15 mm. long, glabrous, flat, somewhat winged by the decurrent blade; leaf-blade elliptic-obovate, thin and membranous, bright green, the largest 17 cm. long by 7 cm. wide, the upper gradually reduced, abruptly narrowed into a rounded, sometimes mucronulate cusp 3 mm. long, minutely denticulate with broad, rounded, callous teeth (3-4 teeth per cm. of margin, barely salient), cuneate or acuminate at base, glabrous; veins plane but conspicuous, the laterals 10-15 mm. apart, ascending at an angle of  $45^{\circ}$ , the veinlets reticulate; inflorescence a subcapitate raceme, soon becoming elongate, the axis hirtellous; floral leaves obovate, persistent, obtuse, scabrellate-pubescent, 15-20 mm. long at anthesis, enlarging to 4-5 cm. long; pedicels slender, hirtellous, equaling the subtending leaves, after anthesis persistent, strongly angled, much thickened, and strongly curved; hypanthium hemispheric, 5 mm. high, 7-8 mm. wide when pressed, sparsely pubescent; sepals somewhat spreading, narrowly triangular, 9 mm. long, 2 mm. wide at base, puberulent, especially on the inner face, separated by narrow but flat sinuses; corolla red, sparsely puberulent, the tube nearly straight, 40 mm. long, the lobes triangular-falcate, 9-12 mm. long; filaments not exerted, glabrous; anther-tube 8 mm. long, glabrous, the two lower anthers with a cartilaginous appendix. FIGS. 7, 8.

Type, *Pennell* 7619, collected 1 July 1922, "San Jose," San Antonio, Dept. El Cauca, Colombia, altitude 2100-2500 m., and deposited in the herbarium of The New York Botanical Garden. Another collection from the same locality is *Pennell & Killip* 7414, 28 June 1922. *Lehmann* 988 is also assigned to this species. In foliage and floral characters, *C. pedicellaris* stands close to *C. grandis* (L.f.) Presl, but is distinguished by its elongate raceme, its longer sepals with flat sinuses, and especially by its persistent thickened pedicels.

The same herbarium contains four sheets collected in the same immediate vicinity at "La Gallera," Micay Valley, two

of them on the same day as the type, in which the leaves are proportionately longer and much more acuminate, the floral leaves narrower and sharply acute, and the raceme less elongate. These may be tentatively considered as a variety of *C. pedicellaris*, under the name *gallerensis* n. var. They are Killip 7701 (type), collected 29-30 June 1922 (duplicate in U. S. Nat. Herb.) Killip 7695, 7948, and 7967.

18. *Centropogon ciliatus* n. sp. Stem, foliage, inflorescence, hypanthium, calyx, and corolla glabrous; stem apparently herbaceous, greenish-brown, somewhat grooved or angled; leaf-blades obovate, deep green, membranous, 14 cm. long, 55-65 mm. wide, abruptly acuminate, cuneate at base into an indefinite petiole as much as 8 mm. long, sharply and finely denticulate-ciliate with triangular, callous-acuminate teeth, interspersed with slender, subulate, callous teeth of the same length (about 16 teeth per cm. of margin, 0.6-1 mm. long); veins barely elevated beneath, the laterals 10-15 mm. apart, broadly divergent and curved-ascending, the veinlets inconspicuously reticulate; inflorescence a subcapitate raceme; floral leaves ovate-oblong, 10-18 mm. long, acuminate, ciliate-denticulate; pedicels 3 cm. long; hypanthium urceolate-hemispheric, 5 mm. long, prominently 5-gibbous above the base; sepals erect, narrowly triangular, 10 mm. long, sparsely denticulate near the tip; corolla bright red, the tube slightly curved, 28 mm. long; filaments not exerted; anther-tube densely hirsute on the dorsal commissures with purple hairs, the two lower anthers with a cartilaginous appendix. FIG. 9.

Type, *Macbride* 4028, collected 23 May-4 June 1923, in dense forests at Muña, Peru, altitude about 7000 feet, and deposited in the herbarium of The New York Botanical Garden (duplicate in herb. Field Museum). The species is distinct within the group *Amplifolii* by its peculiar ciliate-denticulate leaves.

19. *CENTROPOGON AGGREGATUS* (Rusby) Gleason,

Bull. Torrey Club 48: 199. 1921.

*Siphocampylus aggregatus* Rusby, Bull. N. Y. Bot. Gard. 8: 122. 1912.

Bolivia: Rio Machochorisa, near Atén, Dept. La Paz, alt. 3500 ft., *Williams* 1579 (type, herb. N. Y. B. G.), 4 Aug. 1902.

20. *CENTROPOGON SPECIOSUS* Planch. Flore

Serres 6: 16. 1850-51.

Venezuela: Colonia Tovar, *Fendler* 728; Mérida, altitude 6000 ft., *Funck & Schlim* 873 (type, herb. Mus. Paris). Colombia:

La Cumbre, Dept. El Valle, alt. 1550-2000 m., *Pennell* 5150, 7-10 May 1922, *Hazen* 11,821, 11-16 July 1922, *Killip & Hazen* 11,115, 9 Sept. 1922.

21. *CENTROPOGON ALBOLIMBATUS* Wimmer, Repert.  
Spec. Nov. 19: 242. 1924.

Colombia: near Fusagasuga, Dept. Cundinamarca, *Linden* 864 (duplicate of type in herb. Mus. Paris); *Jervise*; *Triana*.

22. *CENTROPOGON PROSTRATUS* Benth. Pl. Hartw.  
212. 1845.

Ecuador: Quito Andes, *Hartweg* 212 (type, herb. Kew).

23. *CENTROPOGON SOLANIFOLIUS* Benth. Pl. Hartw.  
139. 1844.

Ecuador: Mountains of Paccha [Prov. El Oro] *Hartweg* 779 (type, herb. Kew).

24. *CENTROPOGON PLANCHONIS* Zahlbr., Repert.  
Spec. Nov. 14: 133. 1915.

Colombia: Rio Buga, near Cauca, alt. 1600 m., *Lehmann* 776 (type); "Miraflores," Palmira, Dept. El Valle, alt. 1800-2100 m., *Killip* 6144, 27 May 1922; La Cumbre, El Valle, alt. 1600-1800 m., *Killip & Hazen* 11114, 9 Sept. 1922; Popayan, Dept. El Cauca, alt. 1600-1700 m., *Pennell & Killip* 7192, 24, 26 June, 1922; Apia, Dept. Caldas, alt. 1600-1900 m., *Pennell* 10284, 4-5 Sept. 1922; Rio San Rafael, below Cerro Tatama, Caldas, alt. 2200-2400 m., *Pennell* 10321, 7-11 Sept. 1922; "La Virginia," Libano, Dept. Tolima, alt. 1200-1500 m., *Pennell* 3272, 22 Dec. 1917.

#### CENTROPOGON, GROUP AXILLARES

Among the species with axillary flowers and appendiculate anthers, including *C. cornutus* (L.) Druce and *C. oblongus* Benth., the following two undescribed species have been distinguished.

*Centropogon decemlobus* n. sp. Stem shrubby, irregularly grooved and angled or somewhat flattened, glabrous, the internodes eventually 5 cm. long; petioles slender, glabrous, 1 cm. long; leaf-blades membranous, pale green, narrowly ovate, 7-12 cm. long, 3-5 cm. wide, the upper gradually reduced, abruptly acuminate to an obtuse, mucronulate tip, minutely serrulate



with low, appressed or incurved teeth (about 3 teeth per cm. of margin, 0.3 mm. high), abruptly narrowed to a short-cuneate, somewhat inequilateral base, glabrous; lateral veins 7-9 mm. apart, broadly divergent, curved-ascending, the plane veinlets prominently reticulate beneath; peduncles axillary, 8-15 mm. long, closely pubescent, subulately bracteolate near the base; hypanthium hemispheric, 5 mm. high, 8 mm. wide when pressed, glabrous; sepals appressed, ovate-triangular, 2-3 mm. long, 2 mm. wide at the base, acute, entire, glabrous, separated by broad, distinctly convex or semicircular sinuses; corolla red, 45 mm. long, minutely puberulent, the tube 38 mm. long, slightly decurved, the lobes triangular-falcate; filaments exerted 2-5 mm., glabrous; anther-tube glabrous, 8-9 mm. long, the two lower anthers tipped with a cartilaginous appendix. FIG. 10.

Type, *Pennell 10,233*, collected 3 Sept. 1922, San Jose, Dept. Caldas, Colombia, altitude 1500-1800 m., and deposited in the herbarium of The New York Botanical Garden. Another collection is *Pennell 10,603*, Santuario, Dept. Caldas, alt. 2000-2300 m., 13-14 Sept. 1922, bearing depressed-globose fruits, and with most of the leaves sharply acuminate.

***Centropogon Purdieanus* n. sp.** Stem herbaceous, probably climbing, strongly grooved and angled, thinly scabrellate-pubescent, the internodes 2-4 cm. long; petioles slender, 12-15 mm. long, pubescent; leaf-blades oblong-ovate, somewhat falcate, 8-11 cm. long, 3-4 cm. wide, acute, crenulate, with triangular callous teeth between the crenations (about 3-4 teeth per cm. of margin), broadly cuneate to obtuse and somewhat inequilateral at base, sparsely puberulent on both surfaces, especially on the veins beneath; lateral veins 12-18 mm. apart, strongly curved-ascending, anastomosing near the margin, the veinlets plane and reticulate; peduncles axillary, 12-15 mm. long, densely pubescent; hypanthium broadly hemispheric, 5 mm. high, 9 mm. wide when pressed, thinly but closely pubescent; sepals erect or somewhat spreading, broadly triangular, 1.5-2 mm. long and wide, thinly pubescent; corolla 5 cm. long, somewhat decurved, sparsely puberulent, red, the lobes triangular-falcate; filaments glabrous; anther-tube 9 mm. long, glabrous except for a few white hairs near the tip, the two lower tipped with a cartilaginous appendix. FIG. 11.

Type, *Purdie*, collected in the mountains of New Granada, and deposited in the Gray Herbarium. The herbarium at Kew contains six sheets of this species, all collected by Purdie, and probably all duplicates. One bears the number "seeds 640" and some are labeled "woods of Antioquia." The species differs

from *C. decemlobus* Gleason in the conspicuous pubescence which extends to almost every part of the plant.

Recent collections in Ecuador and Colombia also include four undescribed species with axillary peduncles and penicillate anthers.

*Centropogon leucophyllus* n. sp. Stem herbaceous, finely striate, minutely puberulent when young, becoming glabrous on the first expanded internode; petioles 8–20 mm. long, about one third as long as the blade, margined, ciliate; leaf-blades ovate, 35–60 mm. long, 14–28 mm. wide, acute or subacuminate to a blunt tip, crenate (about 4 or 5 teeth per cm. of margin, 0.5 mm. high or less), broadly obtuse to rounded and somewhat inequilateral at base, dull green and glabrous above, pale green and very minutely puberulent beneath; lateral veins 4–6 pairs, mostly approximate toward the base of the blade, strongly ascending, veinlets inconspicuous, scarcely anastomosing; peduncles axillary, 3–5 cm. long, slender, minutely puberulent, subulate-bibracteolate near the base; hypanthium hemispheric, 4 mm. high, 6 mm. wide when pressed, minutely puberulent; sepals widely spreading to subreflexed, oblong-triangular, 8 mm. long, 2.5 mm. wide at base, tapering regularly to the apex, minutely ciliate and puberulent, with 2 or 3 teeth on each side, separated by narrow acute sinuses; corolla purple, tipped with white, minutely puberulent, the tube lightly decurved, about 25 mm. long, the lobes almost straight, the upper oblong, 8 mm. long, the lateral and lower triangular, 5–6 mm. long; filaments not exerted, glabrous; anther-tube 5 mm. long, glabrous, the two lower anthers penicillate; fruit a berry. FIG. 12.

Type, *Pennell 10,490*, collected 8–10 Sept. 1922, Cerro Tatama, Dept. Caldas, Colombia, altitude 3200–3400 m., and deposited in the herbarium of The New York Botanical Garden. Other collections are *Pennell 10,419*, Rio San Rafael, below Cerro Tatama, altitude 2500–2800 m., 7–11 Sept. 1922; *Pennell 9351*, "Pinares" above Salento, Dept. Caldas, alt. 2700–2900 m., 2–10 Aug. 1922; and *Dawe 736*, Ruiz, at Termes, alt. 3000 m., 1918. These specimens are constant in the character of the flower, venation, and pubescence, but differ considerably in the size and shape of their leaves. In Dawe's collection these are broadly ovate, blunt at the apex, truncate or subcordate at base, and not exceeding 25 by 30 mm. in size; in *9351* they are oblong-ovate, as large as 26 by 58 mm.; and in *10,419*, which was noted by the collector as growing in the shade, they are very thin, elongate-ovate, and as large as 46 by 96 mm.

**Centropogon carpinoides** n. sp. Stem herbaceous, glabrous, pale greenish brown or purplish, strongly and irregularly grooved and angled, the internodes mostly 2-4 cm. long; petioles slender, 2-3 cm. long, narrowly margined, minutely puberulent; leaf-blades membranous, triangular-ovate, 5-6 cm. long, 35-45 mm. wide, or the upper notably reduced, broadest near the base, gradually tapering or subacuminate to a blunt apex, broadly cuneate to truncate or subcordate at the inequilateral base, prominently crenate (3-7 teeth per cm. of margin, 0.4-1 mm. high), dull green and glabrous above, minutely pubescent on the veins beneath; lateral veins 4-7 pairs, about half of them approximate in the basal fourth of the blade, strongly ascending, the veinlets inconspicuously reticulate; peduncles numerous, axillary, about 25 mm. long, glabrous, the prominent subulate bracteoles 5 mm. long; hypanthium hemispheric, 5 mm. high, 6 mm. wide when pressed, glabrous; sepals erect or somewhat spreading, foliaceous, triangular-lanceolate, 12 mm. long, 2 mm. wide at base, acuminate, glabrous, reticulately veined, with 1-3 salient callous teeth on each side, separated by narrow acute sinuses; corolla apparently red, tipped with white, thinly puberulent, the tube 3 cm. long, nearly straight, the upper lobes oblong, 9 mm. long, nearly straight, the lateral and lower triangular-falcate, decurved, 6 mm. long; filaments not exserted, glabrous; anther-tube glabrous, 5 mm. long, the two lower anthers penicillate; fruit a globose dry berry, 18 mm. in diameter. FIG. 13.

Type, *Pennell 10,348*, collected 7-11 Sept. 1922, Rio San Rafael, below Cerro Tatama, Dept. Caldas, Colombia, altitude 2400-2600 m., and deposited in the herbarium of The New York Botanical Garden. Closely related to *C. leucophyllus* Gleason, from which it differs in its glabrous stem and leaf-surface, its glabrous hypanthium, its longer, reticulately-veined and glabrous sepals, its narrower petioles, and strongly grooved stem.

Both species are related to *C. erythranthus* Zahlbr., in which the leaves are coarsely and irregularly toothed and distinctly narrowed to the base, and the anthers are villous. It may be noted that the length of the sepals in the type specimen of *C. erythranthus* is only 6-7 mm., instead of 11-13 mm. as stated by Zahlbruckner.

**Centropogon griseus** n. sp. Stems stout, woody, striate, gray with short but close pubescence, the internodes 1-3 cm. long; petioles slender, 12-15 mm. long, densely gray-pubescent or subtomentose; leaf-blades firm, broadly ovate, 4-6 cm. long, 25-35 mm. wide, abruptly acuminate, minutely serrulate with appressed teeth (about 6 teeth per cm. of margin, 0.2 mm. high),

broadly truncate to subcordate below and abruptly cuneate to the petiole, minutely puberulent above, thinly pubescent beneath, especially along the principal veins; lateral veins 4 or 5 pairs, ascending at an angle of about  $45^{\circ}$ , anastomosing near the margin, the veinlets inconspicuous; peduncles axillary, 3-5 cm. long, densely pubescent or subtomentose, callous-bracteolate at the base; hypanthium semi-ovoid, 4 mm. long, densely pubescent; sepals thick, erect, narrowly triangular, 3.5 mm. long, obtuse, densely pubescent; corolla 3 cm. long, thinly puberulent, the tube almost straight, strongly contracted above the base, gradually expanded to the throat, the lobes narrowly triangular-falcate, strongly decurved; filaments exerted about 5 mm., conspicuously villous; anther-tube 7 mm. long, prominently white-villous in the furrows, the two lower anthers penicillate. FIG. 14.

Type, *Rose & Rose 23,383*, collected 6-15 Oct. 1918, Portoviejo, Ecuador, and deposited in the United States National Herbarium. Undoubtedly related to the two preceding species, but sharply distinguished from them by its dense and close pubescence and short sepals.

*Centropogon Hitchcockii* n. sp. Stem simple, erect, 12-18 dm. high, grooved, sparsely tomentulose when young, glabrescent with age, the internodes 5-10 mm. long; petioles slender, sparsely pubescent, 10-12 mm. long; leaf-blades thin, oblong-linear, somewhat falcate, 10-12 cm. long, 13-16 mm. wide, long-acuminate, conspicuously denticulate, with black, callous, salient, subulate teeth (about 7 teeth per cm. of margin, 0.4-0.5 mm. high), long-cuneate to the base, thinly pubescent above with short, flat, crooked, pale brown hairs, pubescent on the veins beneath with the same type of hairs, densely so or tomentulose on the midvein; lateral veins about 1 cm. apart, ascending at an angle of about  $30^{\circ}$ , the veinlets closely but inconspicuously reticulate; peduncles axillary, 8-9 cm. long, tomentulose above to thinly pubescent at the base with crooked hairs, ebracteolate; hypanthium urceolate-hemispheric, 5 mm. high, 8 mm. wide when pressed, prominently ribbed or angled, densely pubescent; sepals recurved, linear, 14 mm. long, thinly pubescent on the outer face and margin, frequently involute, entire, separated by rounded, narrow sinuses; corolla red, softly pubescent with white, red-tipped hairs, the tube slightly curved, 3 cm. long, the lobes triangular-falcate, decurved, the upper 10 mm., the lower 6 mm. long; filaments exerted 10 mm., minutely villous; anther-tube 8 mm. long, densely hirsute, especially distally, with purple hairs, the two lower bearded at the apex. FIG. 15.

Type, *Hitchcock 21,681*, collected 12-13 Sept. 1923, between Cuenca and Huigra, Ecuador, altitude 2700-3000 m., and depos-

ited in the herbarium of The New York Botanical Garden (duplicate in U. S. National Herbarium). The species finds its nearest relative in *C. Sodiroanus* Zahlbr., in which the leaves, although narrow, are proportionately broader, the sepals only 8 mm. long and strictly erect, the foliage and flowers glabrous, and the anther-tube covered with white hairs.

#### SIPHOCAMPYLUS NIVEUS AND TWO RELATED SPECIES

A small group of Andean species of *Siphocampylus* is strikingly characterized by a broadly campanulate, almost regular corolla, with unusually short triangular lobes, and by heavy, rugose leaves densely covered on the lower surface by white or gray tomentum. Three species are represented in the collections of the National Herbarium, the Gray Herbarium, and The New York Botanical Garden, distinguished as follows:

Sepals narrowly oblong, 2-3 mm. wide, 8-10 mm. long. .... *S. Jamesonianus*

Sepals narrowly linear, 1 mm. or less wide, 8-12 mm. long.

Leaves elliptic, broadest at or below the middle, obtuse at the base; corolla somewhat decurved, 12-15 mm. wide at the throat when pressed. .... *S. niveus*

Leaves narrowly oblong-obovate, broadest above the middle, long-cuneate at the base; corolla straight, 20 mm. wide at the throat when pressed. .... *S. Pennellii*

#### SIPHOCAMPYLUS JAMESONIANUS (Presl) A. DC. in DC.

Prodr. 7: 402. 1839; Jameson, Syn. Pl. Aequat. 2:

179. 1865.

*Lobelia Jamesoniana* Presl, Prodr. Monog. Lobel. 36. 1836.

*Lobelia pulverulenta* Hook. Jour. Bot. Hook. 1: 231. pl. 131. 1834; not *L. pulverulenta* Pers.

*Byrsanthes Halliana* Presl, l. c. 42. 1836.

*Siphocampylus Hallianus* Vatke, Linnaea 38: 732. 1874.

Ecuador: Ambato, Prov. Tungurahua, *Pachano* 182, March 1919; *Spruce* 4976. Jameson's type locality was vicinity of Baños, Prov. Tungurahua, alt. 6000 feet.

#### SIPHOCAMPYLUS NIVEUS (Willd.) Vatke, Linnaea

38: 732. 1874.

*Lobelia nivea* Willd.; Roem. & Schult. Syst. 5: 58. 1819.

*Siphocampylus lanatus* Benth. Pl. Hartw. 214. 1845.

Colombia: Bogota, *Bonpland* (type); *Triana 1556*; *Hartweg 1188* (type of *S. lanatus*), Purace, Prov. Popayan [Dept. El Cauca]; *Lehmann 5637*; *Pennell & Killip 6451*, "San Isidro," Purace, Dept. El Cauca, alt. 2200-2500 m., 10-11 June 1922.

*Siphocampylus Pennellii* n. sp. Stem herbaceous, stout, erect, densely white-lanate above, becoming glabrous with age; leaves crowded, the internodes about 1 cm. long, ascending, coriaceous, narrowly oblong-obovate, the largest 15 cm. long by 3.5 cm. wide, the upper gradually reduced to 7 cm. long by 2 cm. wide, rounded at the apex, broadest well above the middle, entire, cuneate at the base, on stout, tomentose petioles 10-15 mm. long, above dull green, glabrous, shining, and strongly rugose with deeply impressed veins, beneath densely white-tomentose; peduncles stout, ascending, 6-12 cm. long, exceeding the subtending leaves, ebracteolate, densely tomentose; hypanthium broadly obconic, 10 mm. high, 5-ribbed, densely tomentose; sepals linear, ascending, 8 mm. long, somewhat involute, densely tomentose on the outside, thinly lanate within; corolla broadly campanulate, densely white-tomentose without, yellowish-white, glabrous, and strongly rugose within; tube about 20 mm. long, 22 mm. wide at the throat when pressed, the lobes erect, broadly triangular-ovate, subequal, acute or subacuminate, the largest 12 mm. long by 10 mm. wide, the smallest 8 mm. long by 9 mm. wide; filaments glabrous, shorter than the corolla lobes; anther-tube gently decurved, 9 mm. long, glabrous or with a few long white hairs in the commissures, all anthers densely bearded at the summit with yellowish hairs; fruit a capsule. FIG. 16.

Type, *Pennell 7509*, collected 29-30 June 1922, on Mount Trompo del Puerco, Dept. El Cauca, Colombia, altitude 2500-2900 m., and deposited in the herbarium of The New York Botanical Garden.

#### SIPHOCAMPYLUS UMBELLATUS AND THREE NEW RELATED SPECIES

SIPHOCAMPYLUS UMBELLATUS (H.B.K.) G. Don,

Gen. Syst. 3: 702. 1834.

? *Lobelia gigantea* Cav. Ic. 6: 9. pl. 513. 1801.

*Lobelia umbellata* H.B.K. Nov. Gen. & Sp. 3: 304. pl. 268. 1818.

*Lobelia ayavacensis* Willd.; Spreng. Syst. 1: 709. 1825.

*Siphocampylus ayavacensis* Steud., Nomencl. ed. 2. 2: 63. 1840.

Until the type specimen of Cavanilles shall have been examined, and its identity with *L. umbellata* H.B.K. established or re-

futed, G. Don's name for this widely variable species had best be maintained. If the two are identical, and it is quite probable they are, the name will become *S. giganteus* (Cav.) G. Don (type locality, between Guaranda and the mountain of San Antonio, Prov. Bolivar, Bolivia). Willdenow's name was a mere manuscript note written by him on a specimen of this species collected by Bonpland at Ayavaca, Dept. Piura, Peru, and doubtless a duplicate of the type of *L. umbellata* H.B.K., apparently in a desire to conserve the name *L. umbellata* Vest, published in 1819.

Few species of the genus are so well represented in herbaria, and but few others show such a wide variation, extending to the proportion and tomentum of the leaves, the amount of pubescence on the anthers, and the length, pubescence, and serration of the sepals. I have not been able to recognize lines of specific demarcation among them. The sheets examined by me are *André 2928*, *Anthony & Tate*, *Bonpland* (3), *Couthoy*, *Hall 57*, *Jameson 238,613*, *Spruce*, *Spruce 5164*, *Triana 1571*, and the following recent collections—Colombia: "Canaan," Mt. Purace, *Pennell & Killip 6500*, 11–13 June 1922; "La Gallera," Micay Valley, Dept. El Cauca, *Killip 7979*, 1 July 1922. Ecuador: "La Rinconada," between Ibarra and Tulcán, Prov. Carchi, *Hitchcock 20,952*, 10–11 Aug. 1923; vicinity of Nabón, Prov. Azuay, *Rose, Pachano & Rose 23,019*, 25 Sept. 1918; vicinity of Cuenca, Prov. Azuay, *Rose, Pachano & Rose 23,806*, 17–24 Sept. 1918; between Cuenca and Huigra, Prov. Canar, *Hitchcock 21,668*, 12–13 Sept. 1923; vicinity of Canar, *Rose & Rose 22,714*, 15 Sept. 1918; Mt. Pichincha, *Mille 359*; Tambillo, Prov. Pichincha, *Mille 375*, Aug. 1923. Altitudes are 2200–3400 m.

The following three species are of the same general affinity, having large coarse flowers, varying from greenish-yellow to nearly white in color, but differing conspicuously in the characters of the hypanthium or calyx.

*Siphocampylus cylindricus* n. sp. Stems suffruticose, 10–15 dm. high, thinly tomentulose above, becoming merely puberulent in age, the internodes 5–15 mm. long; petioles stout, tomentose, 10 mm. long; leaf-blades firm, ovate-elliptic, 20–25 cm. long, 7–9 cm. wide, obtuse, broadly cuneate to an obtuse or subacute base, finely denticulate with blunt, broadly triangular teeth (about 4 teeth per cm. of margin, 0.4–0.6 mm. high), above dark green, rugulose, thinly pubescent with short crooked hairs

on the surface and tomentose along the midvein, beneath closely and roughly brown-tomentulose; lateral veins 6-10 mm. apart, ascending at an angle of  $60^{\circ}$ , frequently branched or anastomosing, the veinlets prominently reticulate above, obscure beneath; peduncles stout, axillary, erect, 14-17 cm. long, brown-tomentulose; hypanthium cylindric above a turbinate base, 20-25 mm. long, 15-17 mm. wide when pressed, thinly tomentulose; sepals erect, stout, linear-lanceolate, 30-35 mm. long, 3 mm. wide at base, tapering regularly to the acuminate subulate tip, prominently spinulose-denticulate with 4-6 black callous teeth 1 mm. long on each side, thinly tomentulose on both sides; corolla greenish-yellow, coarsely tomentose, the tube stout, 17 mm. long, 12 mm. wide at the throat when pressed, the lobes linear-falcate, all strongly decurved, the upper about 32, the lower about 16 mm. long; filaments thinly villous; anther-tube about equaling the upper corolla-lobes, 12 mm. long, densely pubescent in the fissures with stout, somewhat curved, short, brown hairs, the two lower anthers densely bearded with pale, slender, flexuous hairs. FIG. 17.

Type, *Pennell 3142*, collected 17 Dec. 1917 at "Rosalito," Dept. Tolima, Colombia, altitude 2700-3000 m., and deposited in the herbarium of The New York Botanical Garden. A second sheet is *Dawe 740*, Ruiz, Colombia, alt. 3000 m., 1918; *Triana 1582* is certainly closely related and may be the same species.

*Siphocampylus stellatus* n. sp. Stem stout, angled, floccose-tomentulose with brown hairs, the internodes 10-15 mm. long; petioles stout, 5-8 mm. long, tomentose like the stem; leaf-blades firm, narrowly oblong, 9-11 cm. long, 28-32 mm. wide, broadest at or slightly below the middle, obtuse, finely denticulate with black, callous, salient teeth (6-7 teeth per cm. of margin, 0.3-0.4 mm. high), abruptly acute or short-cuneate at base, dark green, rugose, and almost glabrous above, except for short, flat, brown, crooked hairs along the midvein, beneath densely pubescent with the same type of hairs on all veins and veinlets, simulating a tomentose surface; lateral veins widely ascending, lightly arcuate, the veinlets prominently reticulate above, obscure beneath; peduncles axillary, ascending, 10 cm. long, below thinly, above densely stellate-tomentose; hypanthium cylindric above a turbinate base, 15-17 mm. long, 11 mm. wide when pressed, densely stellate-tomentose with brown hairs; sepals linear-triangular, 15-17 mm. long, 3 mm. wide at the base, tapering regularly to the tip, with numerous teeth like those of the leaves, stellate-tomentose; corolla thinly but conspicuously stellate-tomentose, the tube 18 mm. long, the lobes linear-falcate, strongly decurved, the upper 32 mm., the lower 21 mm. long; filaments glabrous; anther-tube 10 mm. long,



densely hirsute on the connectives with orange-yellow, stiff, ascending hairs, the two lower bearded with more slender, longer, somewhat curved hairs. FIG. 18.

Type collected by I. F. Holton, 27 Jan. 1853, between Volcancito and Roble [Old Quindio Trail], Colombia, and deposited in the herbarium of Columbia University at The New York Botanical Garden. Another sheet was collected by Purdie, May 1846, on the flat summit of the Quindio, Colombia. It agrees with the type in every essential feature, but averages a little larger in all dimensions.

*S. stellatus* is obviously closely related to *S. cylindricus* Gleason, but is distinguished at once by the stellate pubescence and short sepals.

*Siphocampylus Hazenii* n. sp. Stem stout, hollow above, irregularly angled, somewhat scurfy, the internodes much abbreviated at the summit; petioles stout, 3-4 cm. long, scurfy like the stem; leaf-blades oblong-elliptic, firm, 20-30 cm. long, 7-9 cm. wide, acute, long-cuneate to the base and somewhat decurrent on the petiole, finely denticulate with low, dark, obtuse, subcallous teeth (3-4 teeth per cm. of margin. 0.4-0.7 mm. high), rugulose and thinly arachnoid-tomentulose above when young, becoming glabrate with age, beneath pale green, densely arachnoid-tomentulose when young, thinly arachnoid at maturity, especially along the veins, and persistently scurfy on the midvein; veins lightly impressed above, prominently elevated beneath, the laterals 6-10 mm. apart, somewhat arcuate, strongly ascending, the veinlets conspicuously reticulate; peduncles stout, axillary, erect or ascending, 12-14 cm. long, thinly arachnoid, glabrescent with age; hypanthium short-cylindric or broadly urceolate, 17 mm. high and wide, thinly scurfy; calyx glabrous, purplish, gamosepalous, 2-lipped, the upper lip 12-15 mm. long, barely united with the lower, which is 25 mm. long; calyx-lobes broadly triangular, erect, acute, 8 mm. long, 6 mm. wide; corolla yellowish, thinly scurfy, its tube shorter than the calyx, about 20 mm. long, lobes linear-falcate, strongly decurved, the upper 30 mm. long, 5 mm. wide; filaments barely exerted, glabrous; anther-tube 13 mm. long, glabrous, strongly decurved at the summit, the two lower anthers densely bearded with crooked hairs. FIG. 19.

Type, Killip & Hazen 12,081, collected 27-30 July 1922, Rio Quindio, near Salento, Dept. Caldas, Colombia, altitude 1500-1600 m., and deposited in the herbarium of The New York Botanical Garden. Other specimens, all from Quindio, so far as noted, are Purdie, Goudot, André 2097, and Linden 1073 (herb. Kew), and Triana 1573 (herb. Mus. Paris).

There are few species of *Centropogon* or *Siphocampylus* with strongly gamosepalous calyx, and this is the only one, so far as known to me, with a corolla like that of the group with the well-known *S. umbellatus* G. Don.

#### NEW SPECIES RELATED TO *S. VOLUBILIS* AND *S. BENTHAMIANUS*

The numerous species of this general affinity are readily recognized in herbarium material, although they are not easy to characterize. They all have large showy axillary flowers, mostly on long peduncles, corollas much constricted just above the base and greatly expanded toward the summit, penicillate anthers, and long-petioled leaves, mostly ovate or cordate in outline. Within their number two well-marked groups may be distinguished. The first of these has a turbinate receptacle, widest at the summit, while in the second the receptacle is more or less pyriform, widest below the summit and conspicuously narrowed to the base of the sepals. Both groups are abundantly represented in herbaria and have frequently been in cultivation, which has led to the publication of several names based solely on greenhouse material. Of the five following species, the first two have the turbinate or obconic receptacle of *S. volubilis* (H.B.K.) G. Don, and the last three have the pyriform receptacle of *S. Benth- amianus* Walp. (*S. cordifolius* Benth.).

***Siphocampylus dentatus* n. sp.** Stem herbaceous, probably climbing, pale greenish-brown, essentially glabrous; internodes 2-4 cm. long; petioles slender, tortuous near the base, 1 cm. long, lengthening to 2 cm. at maturity, thinly puberulent; leaf-blades membranous, ovate, 8 cm. long, 4.5 cm. wide, the upper gradually reduced, long-acuminate, cordate at base, sharply, coarsely, and irregularly dentate with triangular and erect, or falcate and retrorse teeth (about 4 teeth per cm. of margin, 1-2 mm. long), minutely pubescent above when young, soon glabrescent except on the midvein, glabrous on the surface and closely puberulent on the veins beneath; lateral veins 4-5 pairs, the basal widely divergent, the upper strongly ascending, the veinlets obscure, plane, reticulate; peduncles axillary, slender, 4.5 cm. long, sparsely puberulent, subulately bibracteolate at the base; hypanthium broadly obconic, 6 mm. high, 9 mm. wide when pressed, thinly puberulent, prominently 10-nerved; sepals erect or somewhat spreading, foliaceous, narrowly triangular, 14-17 mm. long, 2.5 mm. wide at base, tapering regularly to the apex, prominently hirtellous on the midvein,

conspicuously ciliate, finely reticulate, separated by narrow acute sinuses; corolla rose-pink, thinly puberulent on the ribs, the tube slender, 40 mm. long, 7 mm. wide at the throat when pressed, the lobes linear, 13-18 mm. long; filaments not exceeding the upper corolla-lobes, glabrous; anther-tube 7 mm. long, glabrous, the two lower anthers penicillate. FIG. 20.

Type, *Hazen 9663*, collected 7 Aug. 1922, Rio Coello to San Miguel, New Quindio Trail, Dept. Tolima, Colombia, and deposited in the herbarium of The New York Botanical Garden. Other collections, also from Tolima, are *Killip & Hazen 9621*, between "El Eden" and "La Palmilla," Old Quindio Trail, alt. 1800-2300 m., 8 Aug. 1922, and *Killip 9738*, Rio Paloma, New Quindio Trail, 13 Aug. 1922. *Triana 1539* seems to be also the same species. Most closely related to *S. odontosepalus* Vatke, from which it differs in its triangular, ciliate, entire sepals and its coarsely dentate leaves.

***Siphocampylus pilosus* n. sp.** Stem herbaceous, nearly terete, densely pubescent or subtomentose with pale brown hairs, the internodes 1-3 cm. long; petioles stout, frequently deflexed, 6-10 mm. long, densely pubescent; leaf-blades thin, dull green, ovate, 6-7 cm. long, 3-3.5 cm. wide, broadest below the middle, gradually tapering or subacuminate to a straight or falcate blunt tip, finely and irregularly serrate (about 6 teeth per cm. of margin, 0.2-0.5 mm. high), cordate at base (sinus 2-4 mm. deep), or broadly truncate, sparsely and minutely pubescent above, glabrous in age except along the midvein, densely short-hirsute beneath (hairs straight, 0.3 mm. long), especially along the veins, where the hairs are twice as long; lateral veins 8-10 pairs, nearly straight, ascending at an angle of about 45°, the plane veinlets finely but conspicuously reticulate; floral leaves resembling the cauline, but 25-30 mm. long; peduncles axillary, spreading or deflexed, frequently tortuous, densely pubescent, 10-15 mm. long; hypanthium broadly obconic, 4 mm. long, 8 mm. wide when pressed, densely pubescent, 10-ribbed; sepals spreading or reflexed, linear-oblong, 4 mm. long, blunt, entire, densely pubescent, separated by broad flat sinuses; corolla scarlet, 5 cm. long, thinly pubescent with purple hairs, the tube lightly decurved, much contracted above the base, 7 mm. wide at the throat when pressed, the lobes linear-oblong, acute, the upper 15 mm. long; filaments glabrous, about equaling the upper corolla-lobes; anther-tube 6 mm. long, densely hirsute in the fissures, the two lower anthers penicillate. FIG. 21.

Type, *Rusby & Pennell 680*, collected 1-8 Aug. 1917, east of Neiva, Dept. Huila, Colombia, altitude 2200-2500 m., and de-

posited in the herbarium of The New York Botanical Garden (also Gray Herbarium). Other collections, also from Huila, are *Rusby & Pennell 908*, "Balsillas" on Rio Balsillas, alt. 2000-2300 m., 3-6 Aug. 1917, and *Bro. Ariste-Joseph B-77*, El Gigante, 1920 (U. S. Nat. Herb.). The species differs from *S. hispidus* Benth. in its shorter, entire sepals, its shorter peduncles, and its finely serrulate leaves with shallower basal sinus.

*Siphocampylus venosus* n. sp. A climbing shrub; stems reddish-brown, glabrous, strongly angled or subulate, freely branched above; petioles tortuous, glabrous, 5-8 mm. long; leaf-blades broadly ovate-oblong, firm, 25-40 mm. long, 15-25 mm. wide, abruptly short-acuminate, broadly rounded to truncate or subcordate at base, sharply and irregularly serrate (3-5 teeth per cm. of margin, 1-3 mm. long), glabrous and rugulose with impressed veins above, pale green and glabrous beneath; lateral veins 4-6 pairs, ascending at an angle of about 45°, the purple-black veinlets prominently reticulate; peduncles axillary, stout, somewhat flexuous, glabrous, ebracteolate, 5-8 cm. long; hypanthium obovoid-pyriform, broadest above the middle, 9 mm. long, 7-8 mm. wide when pressed, faintly ribbed, glabrous; sepals erect or slightly recurved at the apex, oblong-triangular, 2-3 mm. long, acuminate, glabrous, separated by rounded sinuses as wide as the sepal; corolla red, 5 cm. long, glabrous, the tube gradually contracted from the base to a width of 1.5 mm., thence expanding to a width of 9 mm. at the throat when pressed, the lobes narrowly triangular, acuminate, 9 mm. long; filaments barely exerted, glabrous; anther-tube dull gray, 8-9 mm. long, glabrous or sparsely pilose with long white hairs, the two lower anthers penicillate. FIG. 22.

Type, *Killip & Hazen 9427*, collected 1-2 Aug. 1922, "Magaña," Old Quindio Trail, Dept. Caldas, Colombia, altitude 3200-3300 m., and deposited in the herbarium of The New York Botanical Garden. A member of the same group with *S. megalanthus* Zahlbr., *S. pubescens* Benth., and *S. Benthamianus* Walp., and differing from all of these by its glabrous foliage and flowers; from related glabrous species it is distinguished by its broad leaves and short sepals. A second collection, apparently representing a shade form, is *Pennell 9359*, also from Caldas, "Pinares" above Salento, alt. 2700-2900 m., 2-10 Aug. 1922.

*Siphocampylus obovoideus* n. sp. Climbing shrub, glabrous except the stamens; stems slender, pale brown, finely striate, the internodes 2-4 cm. long; petioles slender, tortuous, 5-9 mm. long; leaf-blades oblong-lanceolate to triangular-lanceolate,

thin, 40-65 mm. long, 12-18 mm. wide, broadest near the base, long-acuminate from the middle or below it, broadly cuneate to an acute or obtuse base, or rarely truncate, sharply and irregularly serrate with triangular-subulate teeth interspersed with subulate cilia (about 5 teeth per cm. of margin, 1-1.5 mm. long); lateral veins 4 or 5 pairs, ascending at an angle of 30-45°, the veinlets inconspicuously reticulate; peduncles axillary, slender, curved at the summit, 9-11 cm. long; hypanthium obovoid-pyriform, 10 mm. long, abruptly expanded above the middle, faintly ribbed; sepals erect, subulate-triangular above the dilated base, 4 mm. long, separated by broadly rounded sinuses; corolla pink (or carmine-red), 5 cm. long, the tube greatly contracted to 5 mm. above its base, thence gradually expanded and 11 mm. wide at the throat when pressed, the lobes oblong-triangular, abruptly acuminate; filaments exerted about 4 mm., minutely villous on the ventral side; anther-tube 8 mm. long, sparsely pilose with short white hairs, the two lower anthers penicillate. FIG. 23.

Type, *Pennell & Killip 8033*, collected 2 July 1922, San Antonio to Rio Ortega, Dept. El Cauca, Colombia, altitude 2100-2200 m., and deposited in the herbarium of The New York Botanical Garden. A second collection is *Pennell & Killip 5866*, La Cumbre, Dept. El Valle, alt. 1800-2100 m., 21-25 May 1922. Distinguished from *S. venosus* Gleason by its narrower, long-acuminate leaves; from *S. pyriformis* Zahlbr. by its shorter sepals and its serrate leaves cuneate to the base.

*Siphocampylus coronatus* n. sp. Stem apparently woody, the whole plant glabrous except the petioles and anthers; stems pale brown, finely striate, leafy, the internodes 15-30 mm. long; petioles slender, frequently tortuous, 4-8 mm. long, minutely villous on the upper side; leaf-blades thin, dark green, ovate-oblong, 5-7.5 cm. long, 2-3 cm. wide, broadest well below the middle, thence gradually tapering to the acute tip, truncate to subcordate and frequently inequilateral at base, sharply and irregularly serrate with triangular-subulate teeth (about 5-6 teeth per cm. of margin, 1-2 mm. long); lateral veins 5-7 pairs, ascending at an angle of about 60°, the veinlets finely reticulate; peduncles axillary, 6-8 cm. long, slender, mostly curved near the summit, ebracteolate; hypanthium obovoid-pyriform, 9 mm. long, 8 mm. wide when pressed; sepals foliaceous, recurved-spreading, oblong-lanceolate, 9-11 mm. long, long-acuminate, veiny, sharply subulate with triangular-subulate teeth; corolla red, 5 cm. long, the tube greatly contracted 5 mm. above the base, and thence gradually expanded to 11 mm. wide at the throat, the lobes oblong-triangular, acute; filaments

glabrous, exerted about 5 mm.; anther-tube dull gray, glabrous except for a very few long white hairs, the two lower anthers penicillate. FIG. 24.

Type, *Pittier 868*, collected Jan. 1906, above Palmira, Dept. El Valle, Colombia, altitude 1200-1600 m., and deposited in the United States National Herbarium. Its nearest relative is apparently *S. megalanthus* Zahlbr., which has similar long, recurved, but linear sepals, and is generally pubescent on its foliage and flowers. Its foliaceous sepals distinguish it at once from the glabrous members of the group with pyriform hypanthium.

## Explanation of plate 3

FIGS. 1-7, hypanthium, calyx, and base of corolla,  $\times 1.5$ , of

- |                                      |                                      |
|--------------------------------------|--------------------------------------|
| 1. <i>Centropogon congestus</i> .    | 5. <i>Centropogon curvatus</i> .     |
| 2. <i>Centropogon gesnerioides</i> . | 6. <i>Centropogon parvulus</i> .     |
| 3. <i>Centropogon angustus</i> .     | 7. <i>Centropogon pedicellaris</i> . |
| 4. <i>Centropogon serratus</i> .     |                                      |

FIG. 8, pedicel at maturity,  $\times 1.5$ , of *Centropogon pedicellaris*.

FIGS. 9-15, hypanthium and calyx, with or without the base of the corolla,  $\times 1.5$ , of

- |                                       |                                      |
|---------------------------------------|--------------------------------------|
| 9. <i>Centropogon ciliatus</i> .      | 13. <i>Centropogon carpinoides</i> . |
| 10. <i>Centropogon decemlobus</i> .   | 14. <i>Centropogon griseus</i> .     |
| 11. <i>Centropogon Purdieanus</i> .   | 15. <i>Centropogon Hitchcockii</i> . |
| 12. <i>Centropogon leucophyllus</i> . |                                      |

FIGS. 16 and 17, single flower, natural size, of

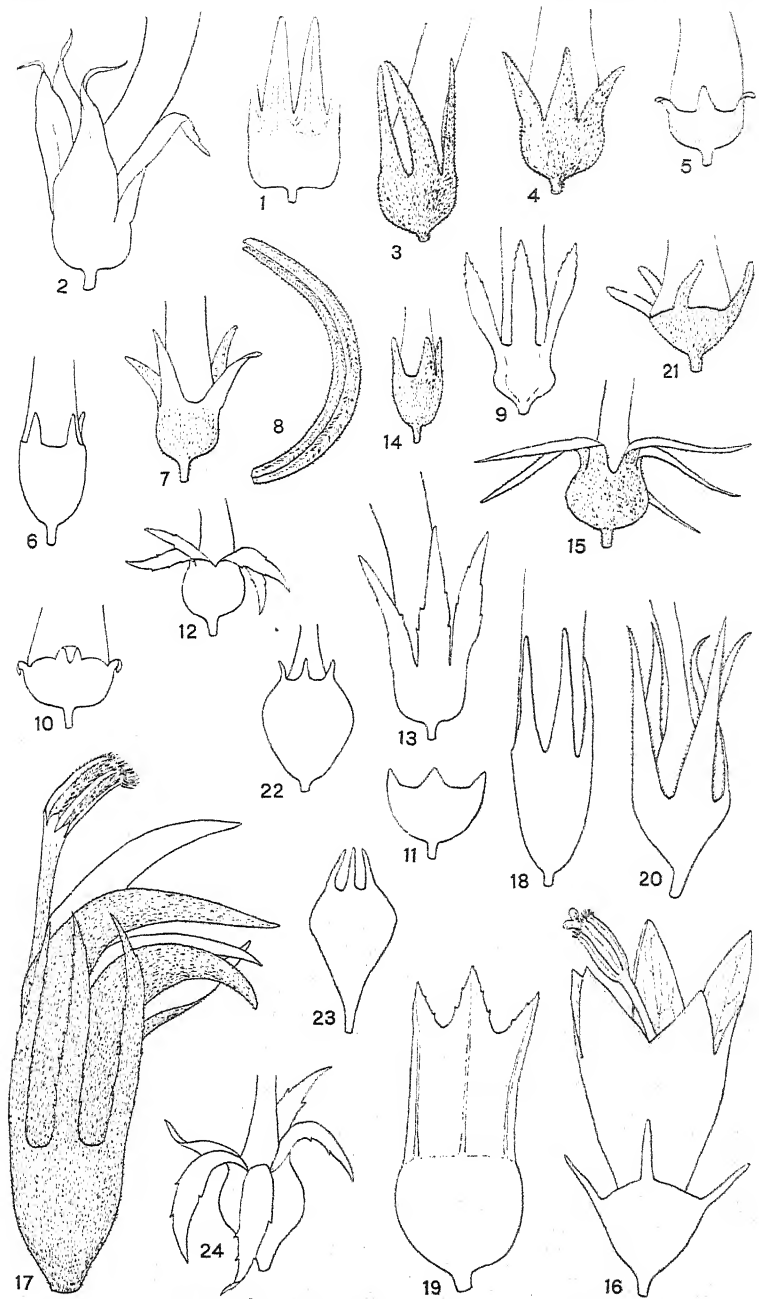
- |                                      |                                        |
|--------------------------------------|----------------------------------------|
| 16. <i>Siphocampylus Pennellii</i> . | 17. <i>Siphocampylus cylindricus</i> . |
|--------------------------------------|----------------------------------------|

FIG. 18, hypanthium, calyx, and base of corolla, natural size, of *Siphocampylus stellatus*.

FIG. 19, hypanthium and portion of calyx,  $\times 1.5$ , of *Siphocampylus Hazenii*.

FIGS. 20-24, hypanthium and calyx, with or without the base of the corolla,  $\times 1.5$ , of

- |                                     |                                       |
|-------------------------------------|---------------------------------------|
| 20. <i>Siphocampylus dentatus</i> . | 23. <i>Siphocampylus obovoideus</i> . |
| 21. <i>Siphocampylus pilosus</i> .  | 24. <i>Siphocampylus coronatus</i> .  |
| 22. <i>Siphocampylus venosus</i> .  |                                       |



CENTROPOGON AND SIPHOCAMPYLUS





# INDEX TO AMERICAN BOTANICAL LITERATURE

1924

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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BULLETIN  
OF THE  
TORREY BOTANICAL CLUB

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MARCH 1925

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Studies of *Lythrum Salicaria*—II\*

A new form of flower in this species

A. B. STOUT

(WITH SIX TEXT FIGURES)

The purple loosestrife, *Lythrum Salicaria* L., has long been known as one of the relatively few species of plants that are trimorphic. That is, the species includes individuals having flowers of three different types. Named with respect to the three lengths of pistils, there are the *long-styled* flowers (see FIG. 5) with a set of long-stamens and a set of short-stamens (enclosed within the calyx and not shown in the picture), the *mid-styled* flowers (FIG. 2) with a set of long-stamens and a set of short-stamens, and the *short-styled* flowers (FIG. 1) with a set of mid-stamens and a set of long-stamens. There is thus one of the three kinds of pistils and two different sets of stamens in each flower. All flowers on a plant are alike. The species includes three groups of individuals or *forms* in regard to the relative length of pistils and stamens as shown in FIGS. 1, 2 and 5.

Students of this species have noted minor variations in respect to structure, size, color, and inter-relations in fertilization among pistils and stamens. All have, however, evidently experienced no special difficulty in grouping the plants which they studied into the three forms generally recognized. No distinctly new form or modification of the old forms seems to have been found. But in a culture of this species recently grown at the New York Botanical Garden, noticeable variations have appeared and one type of flower is sufficiently frequent to be recognized as a new form.

In this new form (see FIGS. 3, 4 and 6) the pistil and the set

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\* Contributions from the New York Botanical Garden, no. 268.

[The Bulletin for February (52: 35-80) was issued 9 March 1925.]



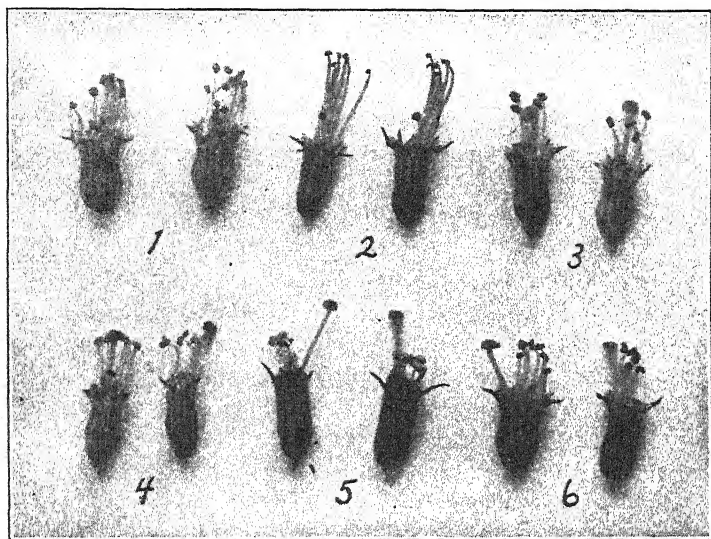
of longer stamens are almost of equal length and this length is about midway between the two lengths characteristic of the mid- and the long-lengths as seen in long- and in mid-styled plants. It is to be noted that the long stamens of the short-styled form (FIG. 1) are as a rule somewhat shorter than are the long stamens of the mid-styled form (FIG. 2). The stigmatic lobes of the pistils of the new form are as large or even larger than those of long-styled plants and considerably larger than the stigmas of mid-styled plants (compare FIGS. 3, 4 and 6 with 5 and 2). The new form may be considered as homomorphic for the lengths of the pistil and the set of longer stamens but there is also a set of short stamens so it may be designated as a semi-homomorphic form.

The first plant having flowers of this new type appeared among the self-fertilized progeny of a mid-styled plant. The other 58 sister plants of this particular series were either mid-styled or long-styled with no marked deviations in lengths of parts from those typical for these forms. This plant was selfed by the bagging method in the first year of its bloom and found to be highly self-compatible. It was then removed to my home garden at Pleasantville, New York, where it was grown in isolation from any other plant of *Lythrum*. It produced seed in abundance to the enforced self-pollinations and from such seed 122 plants have been grown to blooming age, and for many of these, observations on flower character have been made for three years. Of these plants, 60 were readily to be classed as of the new semi-homomorphic form, nine were long-styled, 52 were intermediate between the new form and the long-styled and one plant was mid-styled. The intermediates varied toward the long-styled form in that the pistil was longer than the stamens; there were none that varied toward the mid-styled form.

Mention should be made of the wide variations in the color of anthers in the flowers of these plants. The anthers of long stamens and the pollen which they contain are typically dark colored or purplish, sometimes described as greenish, while the anthers and pollen of short- and mid-stamens are yellow. It has, however, frequently been observed that some of the mid-stamens of long-styled plants may be dark in color.

In the first plant of the new form the various members of the longer set of stamens were quite uniform as to length, but purple

and yellow anthers were intermingled, with the yellow predominating. For most of the 122 plants, the offspring of this first semi-homomorphic plant, the anthers of the *longer set of stamens* were much mixed in color. The summary for the entire series is as follows. For the one mid-styled plant these anthers were uniformly all dark. For the nine long-styled plants, seven had



FIGURES 1-6. Flowers typical for the four forms in the one species *Lythrum Salicaria*. The three older forms are the *short-styled* (1), the *mid-styled*, (2) and the *long-styled* (5). Flowers of the new and *semi-homomorphic* form are shown at 3, 4 and 6; the anthers of the longer set of stamens are all purple in 6, all yellow in 4, and yellow or purple intermingled in 3. The short stamens and pistils are, except in a few cases, entirely enclosed within the calyx. The magnification is almost two times natural size.

only the yellow anthers typical of this form and two had colors intermingled. For the 60 plants of the new form, the long stamens of six were wholly dark (see FIG. 6), 25 were wholly yellow (see FIG. 4) and for 29 there was a mixture of both colors. For the intermediates, only dark stamens were found for six, only yellow for 21, leaving 25 with the colors intermingled. For a large number of plants in this series, the color of the longer set of stamens was highly variable. The relative number of dark and yellow stamens varied greatly for different individuals; it

varied among flowers open on the same day, and it varied from day to day.

Naturally the question arises as to whether plants of the new form are highly self-compatible, or are more decidedly or more uniformly so than are plants of the old form. In them, self-pollinations from pollen of the longer set of stamens are "legitimate." Legitimate pollination is not possible in self-pollinations of any individuals of the three old forms. For them, legitimate pollinations are all inter-form cross-pollinations which as a rule appear to be more productive of fruit and seeds than are illegitimate self- or cross-pollinations in accordance with the results obtained by Darwin (1865 and 1877).

The first plant of the semi-homomorphic form was highly self-compatible not only in the large number of capsules produced but in the high average of seed per capsule and in the viability of the seeds. Twelve plants of its offspring having the new form of flower were tested by controlled self-pollinations; three were highly self-fruitful, five were somewhat self-fertile, and four appeared to be self-incompatible. Another of these plants was grown in isolation and it yielded fine capsules for nearly every flower that bloomed. But also four of the six plants with intermediate flowers which were tested were self-fruitful and one of these was very highly so.

The semi-homomorphic form appears to be highly self-fertile, but the degree varies for individual plants and some are self-sterile. This condition has also been found (Stout, 1923) for other forms and especially for the mid-styled form. The new form appears from the data at hand to be at least as highly self-fruitful as is the mid-styled form.

The appearance of only one plant of the new form among a considerable number of plants together with the fact that this form has not been reported previously suggests a mutation. Its form of flower re-appears in a considerable number of its offspring, so there is an hereditary value to the new character. It does not immediately breed true, so the new form is not at first homozygous.

The new form presents a correlated modification of both the pistil and at least one set of stamens. In the size of the stigmatic lobes there is decided resemblance to the long-pistils; the lengths of both pistil and stamens are modified; in the color of

anthers there is variation between the color of long-stamens and that of mid-stamens, with many, all of the same length, that have the colors intermingled. It may also be stated that this particular series of plants has shown variations in the number of petals of flowers, giving in extreme cases, plants entirely apetalous, a condition not observed thus far for any other culture.

Just what genetical changes are involved in the development of the new form can be determined further only by continued line breeding and by the character of progeny of crosses with the other forms. The large number of intermediates ranging toward the long-styled form suggests a relationship between this form and the mid-styled form from which the new form arose. The semi-homomorphic type of flower, is perhaps a reversion toward a simpler homomorphic type of flower which was without doubt the ancestral type of the species.

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## Anomalies in maize and its relatives—II Many-flowered spikelets in maize

PAUL WEATHERWAX

(WITH FOUR TEXT FIGURES)

The spikelets of maize, like those of its nearest relatives in the tribes Tripsaceae, Paniceae, and Andropogoneae, are structurally two-flowered. The primordia of the two flowers appear in early stages of the development of the spikelet, but the subsequent abortion of parts gives rise to various types of mature spikelet in the different genera, or even in different inflorescences of the same individual. Of the two flowers in a spikelet, the upper is regularly the more advanced in development.

Although the floral structures of maize are characterized by a high degree of variability, this is usually a quantitative matter, concerning only the degree of development or of suppression of parts. But a variation that the writer has recently observed seems to involve a structural change of a more fundamental nature, in that the rachilla of the spikelet is often much more complex, the number of flowers in a spikelet is more than two, and the order of development of the flowers is reversed.

Details of the ancestry of the strain in which the anomaly was found are known only in part. Seeds expected to throw 25 per cent dwarf plants were received from Dr. R. A. Emerson

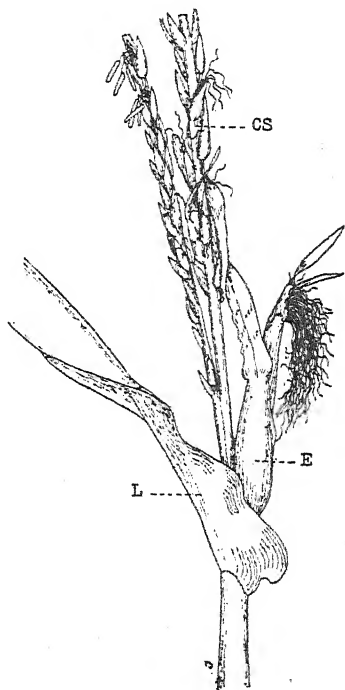


FIG. 1. Terminal inflorescence showing the anomalous spikelets. *L*, uppermost foliage leaf; *CS*, central spike, in the region of the anomalous spikelets; *E*, ear-like modification of a spikelet.

in 1917. This variety has been maintained since then by keeping seed from open-pollinated dwarf plants grown in proximity with their tall half-sisters and other varieties, none of which were dwarfs. In this way a number of homozygous (dwarf) plants could always be had, and the influence of other varieties was eliminated. In 1922, the year before the anomaly appeared,

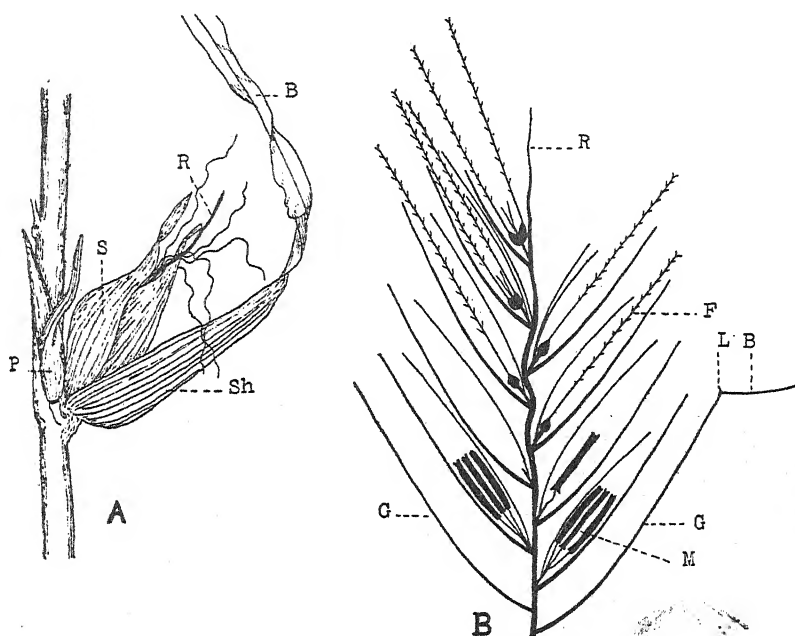


FIG. 2. An anomalous pair of spikelets (A), and the same shown in diagram (B). *S*, sessile spikelet; *P*, pedicelled spikelet; *R*, rachilla; *Sh* (or *G*), *B*, and *L*, sheath, blade, and ligule, respectively, of the lowest glume; *F*, female flower; *M*, male flower.

there was a chance for pollination of the dwarfs with the Chinese waxy variety, a fact which may be significant, in view of the latter's behavior in some crosses (2).

Of fifteen tall plants grown in 1923 from seed grown on a dwarf plant the preceding year, seven showed variously modified spikelets in their tassels. Some of these immediately attracted attention because of their unusual size, and by having three or more protruding silks in many cases. The reversal of sex in maize flowers is sufficiently frequent that a single occur-

rence would have little significance, but two is the maximum number of silks that could be expected from a spikelet unless it had more than two flowers. Dissection of a number of these spikelets showed in most cases more than the two normal flowers, as well as other interesting anomalies.

A typical individual showing the anomaly was selected for detailed examination. This plant bore in the normal position a rudimentary pistillate branch, which did not develop functional

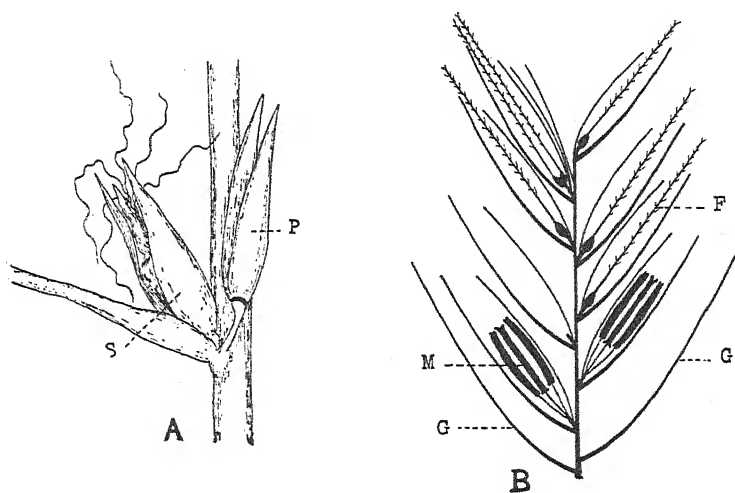


FIG. 3. Another pair of spikelets. Legend the same as in FIG. 2.

flowers. The terminal inflorescence, which was barely exerted from the sheath of the uppermost foliage leaf, consisted of a central spike, a single lateral branch, and a small ear-like structure (FIG. 1).

The many-flowered spikelets occurred on the lower part of the central spike of this tassel. In most cases examined, it was the sessile spikelet of the pair that was modified, but in some instances where the sessile spikelet was extremely modified, the pedicelled member also showed an increase in number of flowers.

Two pairs of spikelets are shown in FIGS. 2, A, and 3, A, and their sessile members in diagram in FIGS. 2, B, and 3, B. The following general peculiarities are noted in these and in other spikelets dissected:



1. The two lowest bracts (glumes) in each spikelet are empty. They may bear ligules and leaf-blades.

2. The lower flowers in the spikelet are the more advanced in development, and the rachilla may be prolonged beyond the uppermost flower (FIG. 2, A and B).

3. The lowest flowers tend to be staminate and the upper pistillate. Between the two kinds may occur more or less incomplete male flowers, or empty lemmas accompanied by paleas.

4. The pistillate flower may be replaced by a pair of flowers, or even by a spikelet or pair of spikelets, with a more or less complete quota of bracts.

5. The alternate arrangement of parts on the rachilla is sometimes apparently interrupted, but this may be due to twisting of the rachilla or to difficulty of observation.

6. The rachilla is sometimes thickened and hardened, bearing the spikelets in horny alveoli, and closely resembling the cob of a four-rowed ear.

7. Fully developed, viable grains are produced in many of the spikelets, the pistillate flowers probably all being fertile.

8. The stamens in these modified spikelets are not exerted at maturity, and are doubtless functionless.

The ear-like structure shown just above the leaf in FIG. 1 is shown again (at maturity) in FIG. 4. It is seen to be associated with a pedicelled structure, the two evidently constituting the equivalent of a pair of spikelets. The structure of this pair (FIG. 4, B and C) shows only a more pronounced expression of the anomaly shown in the preceding cases.

The pedicelled member is a large, normal, staminate spikelet, except that it has three flowers. Here, as in the preceding cases, the stamens are probably functionless.

The sessile member is much like those shown in FIGS. 2 and 3 except in degree of modification. Its bracts are all large and husk-like. One glume and one lemma bear ligules and blades. One lemma subtends a short, rudimentary pistillate spike instead of a flower. Another subtends a pair of pistillate spikelets, each having a full quota of bracts and the aborted lower flower. The rachilla terminates in a well-developed eight-rowed ear, 9 cm. in length. Its two lowest pairs of grains are subtended by the two uppermost, large, well-developed, husk-like lemmas of the spikelet.

Kempton (2) has discussed the phylogenetic significance of

small ears similar to that shown in FIG. 4, which occurred at the base of the tassel in his hybrids involving the Chinese waxy variety and a dwarf (brachytic) strain. But he regards such ears as derivatives of lateral branches of the tassel.

Two or more of the plants of this anomalous population had staminate spikelets whose bracts were in several instances more than 10 cm. long and distinctly leaf-like. In external appearance these spikelets resembled those of the viviparous type figured and described by Collins (1)\*. Although they bore male flowers

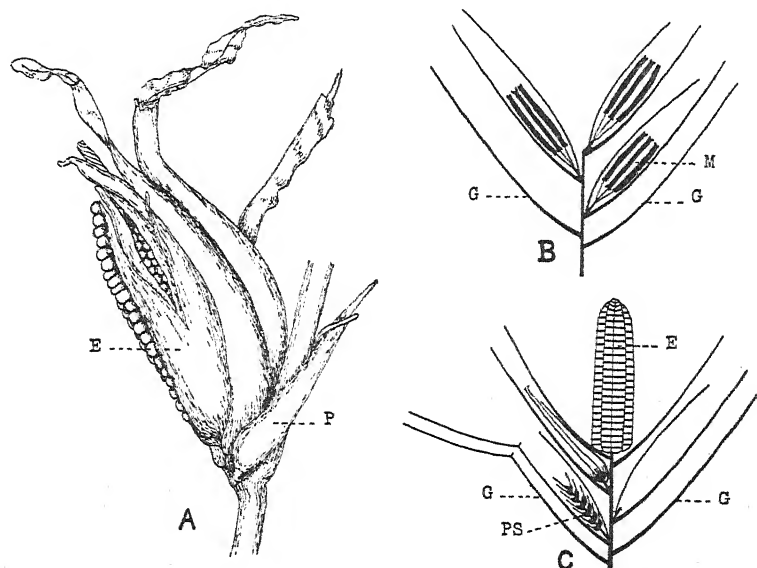


FIG. 4. Another pair of modified spikelets (A), and the pedicelled (B) and sessile (C) members shown in diagram. E, the sessile spikelet, the ear-like structure shown in FIG. 1; P, the pedicelled spikelet; G, glume; M, male flower; PS, pistillate spike.

in their lower portions, their indeterminate nature was evident from the prolonged or embryonic terminal portion of the rachilla. None of the spikelets put out any roots, however, as did those described by Collins.

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\* Collins regards this as a case of apogamy, but it is not at all a parallel of what usually passes under this term. The case that he describes seems to differ in no way from ordinary vivipary, which has been reported in a number of grasses.

The cause of the anomaly is not evident from the data now at hand. It was impossible to self-pollenize any of the plants in 1923, but seeds were produced by open pollination. A greenhouse generation, grown in the winter, showed an apparent recurrence of the anomaly, but the plants were otherwise so modified by the reduced illumination that the results were not dependable. Seeds from the ear shown in FIG. 4 were planted in 1924, but only normal plants were produced. Some of these were selfed, and the characteristic may appear again in the next generation if it is hereditary. Its occurrence in a number of plants at the same time suggests a hereditary or pathological condition. Its apparent recurrence in the greenhouse, and its failure to appear in the same stock in the field, suggests that a specific set of environmental conditions may be necessary for its development.

But, whatever its cause, the occurrence here in the staminate inflorescence, of a series of structures showing all gradations between normal staminate spikelets and almost perfect pistillate shoots might be expected to give some light on the question of the phylogeny of the pistillate inflorescence.

The thing that seems to have occurred in these spikelets, after a reversal in the order of development of parts along the rachilla, is a meristematic reduplication of parts in the spikelet, giving rise to three or more flowers instead of two, and, in extreme cases, replacing flowers with pistillate spikelets or pairs of spikelets arranged in many rows around a cob-like axis.

In other words, the transformation of a two-rowed structure into a many-rowed structure here suggests the possibility of the same occurrence, phylogenetically, in the development of the polystichous axes in the tassel and the pistillate inflorescence from the distichous ancestral form. This is another evidence that it is unnecessary to assume the lateral fusion of spikes to explain the origin of the ear. It does not at all follow from this that the ear is a phylogenetic descendant of the spikelet.

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2. Kempton, J. H. A brachytic variation in maize. U. S. Dept. Agr. Bull. 925: 1-28. *f.* 1-8 + *pl.* 1-19. 1921.

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## Studies on the flora of northern South America—IV\*

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### THE GENUS BURMEISTERA

In 1856 Karsten and Triana established the genus *Burmeistera* to include certain green-flowered, baccate Lobeliaceae of Colombia, and Karsten at the same time published very brief descriptions of several species. The genus was very properly maintained by Bentham and Hooker, but was submerged in *Centropogon* by Schönland in his treatment of the family for the *Natürlichen Pflanzenfamilien*. Zahlbruckner, an exceedingly careful student of the Lobeliaceae, also maintained *Burmeistera* as a distinct genus, but Wimmer, who has more recently begun the study of the family, has again united it with *Centropogon*.

The chief generic distinction between *Siphocampylus* and *Centropogon* has hitherto been found in the character of the fruit, which is capsular in the former and baccate in the latter. If the two genera are to be separated only by this single character, then *Burmeistera*, also with baccate fruit, may well be united with *Centropogon*. But the characters of the corolla seem to be of great importance in distinguishing the genera of Lobeliaceae, and the structure of the anther-appendage, while doubtless of less weight, should by no means be neglected. Five major types of corolla may be discovered in the three genera in question: (1) the *Burmeistera* type, cleft much more deeply on the lower side than on the upper, so that the strongly deflexed lobes appear to be inserted at different heights; (2) the *Centropogon* type, with stout tube, frequently conspicuously bent, and relatively broad, falcate, strongly depressed lobes; (3) the *Siphocampylus* type, with straight slender tube, and relatively narrow, straight or spreading lobes; (4) the *Byrsanthes* type, with short, broad, nearly regular, campanulate tube and short, triangular, erect lobes; and (5) the type of *Siphocampylus radiatus*, with short, broad tube and long, more or less falcate, strongly deflexed lobes. Certain other minor types also exist, but intermediate forms apparently do not occur.

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\* Contributions from the New York Botanical Garden, no. 269.

In *Burmeistera* the two lower anthers are unappendaged. In *Centropogon* and *Siphocampylus* the appendage may consist of a mass of soft crooked hairs, of a tuft of straight, stiff, erect hairs, or of similar hairs concrescent into a flat triangular scale. All of these are represented in *Centropogon*, which is thus seen to be a heterogeneous mixture as to anthers, just as *Siphocampylus* is a mixture as to corolla. The character of the fruit, which is now the sole distinction between two of the genera, does not appear to be constant and certainly does not merit the importance which has been attached to it. Most specimens in herbaria are without fruit and many species have been described without the fruit being seen, yet any of them may be assigned easily and accurately to their proper place by the character of the corolla and anthers alone.

The scope of a genus depends, of course, entirely upon personal opinion. No one can speak *ex cathedra*, defining the extent of any genus or specifying what characters are to be used in generic segregation. Yet anyone who examines a series of plants of this group will observe as great structural differences within the single genus *Siphocampylus* as between any part of it and the genus *Centropogon*. If the existing and easily observable characters are given proper consideration, but two courses are logically available. If the various types of corolla and of anther-appendage are not regarded as of generic value, then *Burmeistera*, *Centropogon*, and *Siphocampylus* should be united into one vast genus. If they are of generic value, at least five genera should be recognized instead of three. The former course is at variance with current usage and current taxonomic practice, and either of them would necessitate, if adopted, the alteration of scores of binomials, thereby adding permanently to an already unwieldy synonymy and affecting the names of numerous species now in horticultural trade. Taxonomists would be well advised to avoid throwing any of their burden of synonymy upon those who use plants or upon those engaged in other lines of botanical activity.

From a practical standpoint it has seemed more desirable to pursue a middle course and maintain the three genera of long standing, while recognizing that two of them are polymorphic groups and might easily be segregated. The result of this treatment is seen in the facts that only one transfer of name is re-

quired and only two double citations appear among twenty-two species.

The center of distribution of *Burmeistera* is the Andes Mountains of Colombia. The genus extends thence south to Peru, east into the Andes of western Venezuela, and north, well into Central America, always at a considerable altitude. The lowest altitude noted on our specimens is 1400 meters, the highest 3000 meters. The species are herbs or shrubs, apparently varying with the size or age of the individual, and a few have been noted as climbing. Since they are not known to twine or produce true holdfast roots, they probably merely recline against the branches of shrubs or trees above them, or take root in moist crevices of the bark.

Seventeen species are known to me from northern South America, and may be distinguished by the key below. Five others have been described but have not been seen by me, while at least five other well-marked but undescribed species are conserved in various European herbaria. In the citation of specimens, the various herbaria are indicated as follows: (G) Gray Herbarium of Harvard University; (K) Royal Botanic Garden, Kew, England; (P) Muséum d'Histoire Naturelle, Paris, France; (W) National Herbarium, Washington, D. C.; (Y) New York Botanical Garden. I have also seen the types of several of Zahlbruckner's species, on loan to the Royal Botanic Garden at Kew.

1. Hypanthium during anthesis obconic to cylindric, conspicuously narrowed to the base, longer than wide when pressed.

Leaves lanceolate, long-acuminate to the sharp tip.

Sepals triangular, acute, separated by narrow acute sinuses; leaves glabrous beneath, the lateral veins strongly ascending and almost parallel to the mid-vein.....

1. *B. Weberbaueri*

Sepals linear or linear-oblong, obtuse or rounded, separated by rounded sinuses; leaves pubescent beneath, the lateral veins widely spreading.

Sepals 10-13 mm. long, exceeding the hypanthium; leaf-pubesence of straight white hairs.....

2. *B. truncata*

Sepals 3-4 mm. long, shorter than the hypanthium; leaf-pubesence of long (0.5 mm.) brownish hairs on the veins and of minute brown hairs on the surfaces.....

3. *B. longifolia*

Leaves oblong to ovate, abruptly narrowed to a cuspidate tip, acute or obtuse.

- Sepals as broad as long and not exceeding 2.5 mm. in length . . . . .
- Leaves sharply and prominently callous-dentate, the lateral veins connected into a prominent marginal vein paralleling the margin at a distance of 2 mm. and strongly elevated beneath . . . . . 4. *B. marginalata*
- Leaves barely denticulate to entire, the lateral veins not connected into a prominent elevated intramarginal vein.
- Sepals acute; leaves oblong or oblong-lanceolate, obtuse at the apex of the cusp . . . . . 5. *B. cylindrocarpa*
- Sepals broadly rounded; leaves ovate or ovate-oblong, sharply acute . . . . . 6. *B. glauca*
- Sepals linear or oblong, notably longer than broad.
- Sepals 2.5-4 mm. long.
- Sepals 1 mm. wide, entire; leaves narrowed to the base . . . . . 8. *B. crispiloba*
- Sepals 1.5-2.5 mm. wide, frequently crenate; leaves obtuse or rounded at the base . . . . . 9. *B. leucocarpa*
- Sepals 12-25 mm. long . . . . . 12. *B. succulenta*
2. Hypanthium during anthesis subglobose or short-cylindric, rounded at the base.
- Sepals ovate, varying to obovate or oblong, shorter than or barely exceeding the hypanthium, 2-4 mm. wide and rarely more than twice as long.
- Leaves broadly round-ovate, thick and firm, strongly rugose above with deeply impressed veins . . . . . 13. *B. Killipii*
- Leaves ovate to oblong or elliptic, thin, not rugose.
- Leaves densely pubescent with minute hairs on the veins beneath.
- Sepals 4-6 mm. long; leaves minutely denticulate . . . . . 14. *B. multiflora*
- Sepals 12-14 mm. long; leaves sharply serrate . . . . . 15. *B. Pennellii*
- Leaves glabrous beneath.
- Leaves broadest above the middle, prominently denticulate, long-cuneate at base . . . . . 16. *B. connivens*
- Leaves broadest below the middle, entire or with minute intramarginal callosities, obtuse at base . . . . . 17. *B. glabrata*
- Sepals linear, longer than the hypanthium, and usually more than three times as long as wide.
- Leaves long-acuminate, usually coarsely repand-serrate . . . . . 19. *B. lacerata*
- Leaves obtuse, acute, or abruptly cuspidate, the callosities almost entirely intramarginal.
- Leaves thick and firm, broadly cuneate to subrotund at base, pubescent on the purplish, conspicuously reticulate veins beneath; intra-

marginal vein prominent; total length of flower about 25 mm..... 21. *B. carnosae*

Leaves membranous, rounded to subcordate at base, glabrous; veins white beneath, faintly reticulate; intramarginal vein obscure; total length of flower about 40 mm..... 22. *B. asclepiadea*

1. *B. WEBERBAUERI* Zahlbr. Bot. Jahrb. 37: 451. 1906.

Peru: *Weberbauer* 2203 (type), mountains east of Huacapistana, alt. 3200 m., Prov. Tarma, Dept. Junin; 2473; *Lobb* 377 (K); *Pearce* (K).

2. *B. TRUNCATA* Zahlbr. Repert. Spec. Nov. 13: 531. 1915.

Ecuador: *Sodi* 91/23 (type), Quito Andes, on the descent from Canzacato to S. Florencio, Prov. Pichincha.

3. *Burmeistera longifolia* n. sp. Stem herbaceous, faintly striate, thinly puberulent with curved slender hairs nearly 1 mm. long, the internodes 1-2 cm. long; petioles 5 mm. long, puberulent, especially on the back; leaf-blades thin, dark-green, narrowly lanceolate, the largest 95 mm. long by 23 mm. wide, the upper gradually reduced to 28 mm. long, long-acuminate, subentire, broadly cuneate or obtuse at base, the veinlets somewhat enlarged and callous at the margin at intervals of about 1 cm., minutely puberulent above when young, scabrellate on the surface at maturity but persistently puberulent along the midvein, thinly pubescent on the veins beneath, lateral veins ascending; hypanthium broadly obconic, 7.5 mm. high, sparsely puberulent; sepals reflexed, narrowly oblong-triangular, 3.5 mm. long with 1 or 2 low callous crenations on each side, puberulent, obtuse, separated by broad rounded sinuses; corolla very sparsely puberulent, the straight tube 14 mm. long on the lower side, 20 mm. on the upper, the lower lobe 8 mm. long, 3 mm. wide, the lateral lobes broadly triangular, 8 mm. long, 6 mm. wide, acute, abruptly decurved at the apex, the upper lobes oblong-falcate, 13 mm. long, 4 mm. wide; filament-tube 37 mm. long, glabrous; anther-tube decurved, 5 mm. long, sparsely puberulent on the sutures, villous with short hairs at the tip.

Type, *Pennell* 4399, collected 7-11 Sept. 1922, in a forest above Cascada Chorrón, south of Antizales, Dept. Bolívar, Colombia, alt. 2400-2700 m., and deposited in the herbarium of the New York Botanical Garden.

4. *B. MARGINATA* Karst. Linnaea 28: 445. 1856.

Colombia: *Triana* 1585 (type, P), vicinity of "Consota" in



Quindio, alt. 1350 m. (near Pereira, Dept. Caldas); *André* 3439 (K).

5. *B. CYLINDROCARPA* Zahlbr. Repert. Spec. Nov. 13: 533. 1915.

Ecuador: *Lehmann* 192 (type), western slopes of Quito Andes near Angui, alt. circ. 1800 m., Prov. Pichincha.

6. *Burmeistera glauca* (Wimmer) n. comb.

*Centropogon glaucus* Wimmer, Repert. Spec. Nov. 19: 251. 1924.

Panama: *Pittier* 3219 (type, W), humid forest of Cuesta de las Palmas, southern slope of Cerro de la Horqueta, Chiriqui, alt. 1700-2100 m. Colombia: *Pennell* 4440, forest, Antizales, Dept. Bolivar, alt. 1700-2000 m., 25, 26 Feb. 1918 (Y); *Pennell* & *Killip* 5798, forest above La Cumbre, Dept. El Valle, alt. 2000-2200 m., 14-19 May 1922 (Y); *Killip* 11,394, bushy summit of west peak, La Cumbre, Dept. El Valle, alt. 2100-2400 m., 11, 18 Sept. 1922 (Y); *Pittier* 742, Cuesta de Tocota, road from Buenaventura to Cali, western Cordillera, alt. 1500-1900 m., Dept. El Valle, Dec. 1905 (W).

7. *B. SODIROANA* Zahlbr. Repert. Spec. Nov. 13: 534. 1915.

Ecuador: *Sodiro* 91/25, along Rio Pilatón, Prov. Pichincha, alt. 900-1600 m. Not seen: from Zahlbruckner's description apparently related to *B. glauca*.

8. *B. CRISPILOBA* Zahlbr. Repert. Spec. Nov. 13: 528. 1915.

Ecuador: *Sodiro* 91/24 (type), subtropical forest of the valley of Pallatanga, Prov. Chimborazo; *André* (K).

9. *B. LEUCOCARPA* Zahlbr. Repert. Spec. Nov. 13: 529. 1915.

Ecuador: *Sodiro* 91/21 (type), temperate forests near S. Florencio and Niebly, Prov. Pichincha; *Pachano* 177, Ambato, Prov. Tungurahua (Y, W); *Jameson* 64, 645, 707, all from Pichincha (K).

10. *B. CERASIFERA* Zahlbr. Repert. Spec. Nov. 13: 532. 1915.

Colombia: *Lehmann* 2934, border of dense forests in the plain of the lower Rio Dagua, Dept. El Valle, alt. 100-300 m. Not seen: from the original description apparently related to *B. crispiloba*. The exceptionally low altitude of this species is noteworthy.

11. *B. RESUPINATA* Zahlbr. Repert. Spec. Nov. 13: 530. 1915.

Ecuador: *Sodire* 91/20, cliffs along Rio Pilatón, Prov. Pichincha, alt. 1000-1600 m. Not seen: from the original description apparently related to *B. leucocarpa*.

12. *B. SUCCULENTA* Karst. Linnaea 28: 445. 1856.

*Centropogon longipes* Zahlbr. Ann. Naturh. Hofmus. Wien. 6: 439. 1891.

Venezuela: Caracas, *Funck & Schlim* 442 (P), *Linden* 231 (K, P); vicinity of Colonia Tovar, *Fendler* 731 (G, K, Y), *Pittier* 9317 (W, Y); *Pittier* 8120, headwaters of Rivers Chichiriviche and Petaquire, Coastal Range, Federal District, alt. 1800-2000 m., 4 Sept. 1918 (W). Colombia: *Triana* 1586 (type, P), "Mariquita Prov. Col." [probably Mariquita, Dept. Tolima]; *Holton* (Y); *Pennell* 5151, forest, La Cumbre, Dept. El Valle, alt. 1800-2000 m., 7-10 May 1922 (Y); *Pennell* 10,685, edge of woods, San Clemente, Dept. Caldas, alt. 1800-2200 m., 16 Sept. 1922; *Pennell & Killip* 5783, forest above La Cumbre, Dept. El Valle, alt. 2000-2200 m., 14-19 May 1922. Ecuador: *Jameson*, Quito (K); *Spruce* 6212, base of Mt. Chimborazo (K).

13. *Burmeistera Killipii* n. sp. Stem shrubby, finely striate, pubescent with scattered, flat, lanceolate, brown hairs, the internodes about 15 mm. long; petioles stout, 7 mm. long, channeled above, pubescent like the stem on the back; leaf-blades dull green, coriaceous, broadly ovate, 20-30 mm. long, 17-25 mm. wide, obtuse or subacute, broadly rounded or subcordate at base, minutely serrate with low, callous, ascending teeth 3-4 mm. apart, glabrous with deeply impressed, arcuately ascending veins above, sparsely pubescent beneath, especially on the prominent veins, with spreading crooked hairs nearly 1 mm. long; peduncles from the upper axils, stout, spreading, 10-15 mm. long, sparsely pubescent, becoming more densely pubescent toward the summit; hypanthium depressed-globose, 5 mm. long, pubescent with brown crooked hairs 0.5 mm. long; sepals firm, reflexed, obovate-oblong, 4 mm. long, 2.5 mm. wide, rounded at the apex, sparsely ciliate, glabrous on the surface; corolla-tube glabrous, 12 mm. long below, 18 mm. long above; corolla-lobes acute, strongly depressed, sparsely pubescent, the lower ovate-lanceolate, 6 mm. long, the lateral triangular-ovate, 6 mm. long, 4 mm. wide, the upper triangular-oblong, falcate, 8 mm. long, 4 mm. wide; androecium glabrous; filament-tube long-exserted, 38 mm. long; anther-tube 3 mm. long.

Type, *Killip 7980*, collected in the forest at "La Gallera," Micay valley, Dept. El Cauca, Colombia, alt. 2200-2500 m., 1 July 1922, and deposited in the herbarium of the New York Botanical Garden; *Pennell 7527*, shrub-zone, Mount El Trueno, Dept. El Cauca, alt. 2700-3000 m., 29-30 June 1922(Y).

14. *B. MULTIFLORA* Zahlbr. Repert. Spec. Nov. 13: 530. 1915.

Ecuador: Quito Andes, *Jameson 542* (duplicate of the type, P); *André 3088* (K).

15. *Burmeistera Pennellii* n. sp. Stem apparently herbaceous, finely striate, pale green, sparsely pubescent when young with spreading white hairs 0.4 mm. long, becoming glabrous with age, the internodes 3-5 cm. long; petioles stout, compressed, 15-25 mm. long, pubescent like the stem; leaf-blades elliptic-oblong, thin and membranous, deep green, 18 cm. long, 7.5 cm. wide, the uppermost smaller, broadest about the middle, abruptly narrowed into a subacuminate or short-cuspidate tip, sharply denticulate with low, broadly triangular, callous teeth (about 3-4 teeth per centimeter of margin), acute at base, minutely puberulent on the surface above, more densely so on the midvein, softly pubescent on the veins and veinlets below with minute spreading hairs 0.4 mm. long, lateral veins widely spreading, nearly straight; peduncles from the upper axils, erect, strongly compressed, 8 cm. long, minutely puberulent; hypanthium subglobose, 9 mm. high, sparsely puberulent; sepals erect, narrowly ovate-oblong, 12-14 mm. long, 3-4 mm. wide, obtuse, sparsely puberulent, conspicuously ciliate, with about 6 pairs of callous, barely protuberant teeth; corolla sparsely puberulent, the tube 7 mm. long below, 15 mm. long above, the lobes narrowly triangular-falcate, the terminal 16 mm. long; filament-tube 23 mm. long, puberulent or subtomentose with yellow hairs; anther-tube glabrous, bright yellow, minutely villous at the orifice.

Type, *Pennell 12,119*, collected near the Rio San Rafael, below Cerro Tatama, Dept. Caldas, Colombia, alt. 2500-2700 m., 7-11 Sept. 1922, and deposited in the herbarium of the New York Botanical Garden.

16. *Burmeistera connivens* n. sp. Stem apparently herbaceous, faintly striate, glabrous to minutely scabrellate, the internodes about 3 cm. long; leaves membranous, dark green, obovate-oblong, 11 cm. long, 4 cm. wide, or the upper smaller, abruptly narrowed above into an acute or subacuminate tip, gradually attenuate at base into a poorly defined, winged petiole, sharply denticulate with low callous teeth (3-4 teeth per centimeter of margin, 0.5 mm. high), glabrous, or with a few slender hairs on

the veins beneath, the lateral veins arcuately ascending, the veinlets conspicuously reticulate beneath; peduncles from the upper axils, slender, compressed, glabrous, 4-5 cm. long; hypanthium short-cylindric, 4-5 mm. high, 3-4 mm. wide when pressed, glabrous, rounded at the base; sepals erect, firm, ovate-oblong, 6 mm. long, 3 mm. wide, obtuse, conspicuously crenulate, somewhat narrowed to the base, glabrous, separated by narrow, acute sinuses; corolla essentially glabrous, about 20 mm. long; filament-tube puberulent, 35 mm. long; anther-tube glabrous, minutely villous at the orifice, 7 mm. long.

Type collected by *Lehmann* in the central Andes of Popayán, Dept. El Cauca, Colombia, alt. 3000-3300 m., distributed by the Bentham Trustees as number 1186, and deposited in the herbarium of the New York Botanical Garden (also G).

17. *B. GLABRATA* (H.B.K.) Benth. & Hook.; B. D. Jackson, Ind. Kew. 1: 361. 1895.

*Lobelia glabrata* H.B.K. Nov. Gen. & Sp. 3: 307. 1818.

*Siphocampylus glabrata* G. Don, Gen. Syst. 3: 702. 1834.

*Centropogon glabratus* Planch. & Ørsted, Vidensk. Meddel. 1857: 157. 1857.

Colombia: *Bonpland* (type, P), near Bogota, alt. 1650 m.; *Pennell* 2392, moist forest, El Peñon, southwest of Sibate, Dept. Cundimarca, alt. 2800-2900 m., 13 Oct. 1917 (Y).

18. *CENTROPOGON RUBROSEPALUS* Wimmer, Repert. Spec. Nov. 19: 252. 1924.

Ecuador: near Quito. Not seen: according to the original description apparently related to *B. glabrata*.

19. *B. LACERATA* Karst. Linnaea 28: 445. 1856.

*B. ceratocarpa* Zahlbr. Repert. Spec. Nov. 13: 534. 1915.

Colombia: *André* 3046 (K); *Linden* 1071, Quindio (P, probably the type); *Pennell* 10,323, clearing, Rio San Rafael, below Cerro Tatama, Dept. Caldas, alt. 2200-2400 m., 7-11 Sept. 1922 (Y), 10,421, along stream in forest, alt. 2500-2800 m., same locality and date (Y), 5148, forest, La Cumbre, Dept. El Valle, alt. 1800-2100 m., 7-10 May 1922 (Y); *Pennell & Killip* 5773, forest above La Cumbre, alt. 1800-2100 m., 14-19 May 1922 (Y); *Killip & Hazen* 11,164, forest, La Cumbre, alt. 1700-2100 m., 9 Sept. 1922 (Y); *Pennell & Killip* 7229, wooded vale west of Rio

Sucio, Dept. El Cauca, alt. 1500-1600 m., 27 June 1922 (Y), 7240, hillside thickets east of Rio Ortega, Dept. El Cauca, alt. 1500-1700 m., 27 June 1922 (Y), 8063, along stream, Rio Ortega, north of Tambo, alt. 1900-2100 m., 2 July 1922 (Y); Killip 7770, forest, "La Gallera" Micay valley, Dept. El Cauca, alt. 1400-1500 m., 29-30 June 1922 (Y), 7942, forest, "La Gallera," alt. 1900-2000 m., 1 July 1922 (Y), 7955, same place and date, alt. 2000-2200 m., (Y), 7862, open land west of Rio San Joaquin, Dept. El Cauca, alt. 1400-1500 m., 29-30 June 1922 (Y); Lehmann B. T. 1074, Popayán (Y), B. T. 1076, Capilla, near Popayán, Dept. El Cauca (Y), 5767, Couga, western Andes of Popayán, alt. 1700-2100 m. (duplicate of type of *B. ceratocarpa*, Y). Ecuador (?): Spruce 5376 (K).

The species presents a considerable variation in foliage, as might be expected from so common a plant.\* Zahlbruckner's *B. ceratocarpa* seems to be only a somewhat xerophytic form.

20. *B. SYLVICOLA* Zahlbr. Repert. Spec. Nov. 13: 532. 1915.

Colombia: Lehmann 2990, dense humid forests of the Cordillera occidental, in the heights of Cali, Dept. El Valle, alt. 2000 m. Not seen: according to the original description apparently related to *B. lacerata*.

21. *Burmeistera carnos*a n. sp. Stem herbaceous, minutely puberulent with appressed hairs when young, glabrescent with age, persistently and densely pubescent at the base of each peduncle, the internodes 10-15 mm. long; petioles stout, 8 mm. long, essentially glabrous, strongly channeled above; leaf-blades elliptic-oblong, thick and somewhat fleshy, dull green, frequently tinged with red beneath or at the margin, the largest 13 cm. long, 4.5 cm. wide, the upper smaller, short-acuminate, broadly cuneate to subrotund at base, glandular at the margin, the glands (about 4 per centimeter of margin) occasionally protuberant

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\*Editor's note. In view of Dr. Gleason's characterization of *G. lacerata* as "so common a plant," it is a matter of surprise and disappointment to the editor, as a member of the Colombian Expedition of 1922, that this species was not found by us in the type region, the Quindio, where much time was spent in intensive collecting. It is even more disappointing that though two members of the Expedition, in going over the Old Quindio Trail to Ibagué, passed through "La Pamilla," the type station for Karsten's unknown *B. ibaguensis*, no *Burmeistera* was found on that trip. This failure can hardly be ascribed entirely to the fact that this genus is characterized by inconspicuous green flowers.

into low teeth, glabrous above, minutely puberulent on the purplish veins beneath, the veinlets prominently reticulate; peduncles from the upper axils, stout, divergent, glabrous, 4-5 cm. long; hypanthium subglobose, 5 mm. high, glabrous; sepals widely spreading or somewhat reflexed, linear, 13-18 mm. long, glabrous, finely veined, acute, frequently purple at the margin or base, with 3 or 4 pairs of minute teeth; corolla glabrous, the tube 8 mm. long below, 13 mm. above, lateral lobes broadly triangular-falcate, 8 mm. long, upper lobes linear-falcate; filament-tube minutely puberulent, 23 mm. long; anther-tube 6 mm. long, glabrous, villous at the orifice; fruit subglobose.

Type, *Pennell & Killip 7325*, from a wet glen in the forest. "San Jose," San Antonio, Dept. El Cauca, alt. 2400-2700 m., 28 June 1922, deposited in the herbarium of the New York Botanical Garden. Other collections from Colombia are *Pennell 4384*, forest above Cascada Chorrón, south of Antizales, Dept. Bolívar, alt. 2400-2700 m., 25 Feb. 1918 (Y), *9405*, wet place, edge of forest, "Pinares," above Salento, Dept. Caldas, alt. 2700-2900 m., 2-10 Aug. 1922 (Y), *12,142*, shrub zone, Mount E' Truena, Dept. El Cauca, alt. 2700-3000 m., 29-30 June 1922 (Y)

22. *Burmeistera asclepiadea* n. sp. Stem suffrutescent, glabrous, ridged, the internodes about 8 cm. long; petioles stout, glabrous, 10-12 mm. long; leaf-blades deep green, thin, broadly ovate-oblong, the largest 14 cm. long, 7.5 cm. wide, the upper smaller, abruptly short-acuminate, broadly rounded or subcordate at base, entire, but with intramarginal callosities (1-2 per centimeter of margin), glabrous above, very minutely puberulent beneath; peduncles from the upper axils, slender, divergent, glabrous, 5-6 cm. long when fully grown; hypanthium subglobose, glabrous, faintly ribbed, 5 mm. high; sepals widely spreading or partly reflexed, green, linear, 15 mm. long, 2 mm. wide, obtuse, entire, with a few intramarginal callosities, glabrous, inconspicuously 3-nerved; corolla glabrous, the tube 16 mm. long above, half as long below, the lobes narrowly triangular-falcate, the terminal 14 mm. long; filament-tube 30 mm. long, sparsely subtomentose with gray hairs; anther-tube stout, 5 mm. long, gray, thinly puberulent; fruit apparently globose.

Type, *Rusby & Pennell 793*, collected in a forest at "Balsillas," on the Rio Balsillas, Dept. Huila, Colombia, alt. 2100-2200 m., 3-5 Aug. 1917, and deposited in the herbarium of the New York Botanical Garden. A second specimen is *Rusby & Pennell 681*, forest, Cordillera oriental, east of Neiva, Dept. Huila, alt. 2200-2500 m., 1-8 Aug. 1917 (Y).

*Burmeistera acuminata* Karst. *Linnaea* 28: 445. 1856, *B. ibaguensis* Karst. *l. c.* 444, and *B. pomifera* Karst. *l. c.* 445, were briefly and inadequately described and are unknown to me. *B. tomentosula* Karst. (*l. c.* 445) also has not been seen by me, but is supposed from the description to belong to the genus *Centropogon*, section *Burmeisteroides* (cf. Bull. Torrey Club 51: 447. 1924.).

## The genus *Hymenopappus* in Colorado

GEORGE E. OSTERHOUT

The genus *Hymenopappus* is a difficult one to study because the characters by which the several species are distinguished are not directly evident. There is a great similarity in the heads of flowers and in the foliage. Hence the achenes and the florets have been carefully examined for characters by which to group the species. The following synopsis has little of originality in it, but the grouping of the species differs from the manner in which it has been customary to arrange them, and is offered as a study in the genus.

1. Throat of the corolla campanulate, 1.5-2 mm. long.  
Paleae of the pappus very short and hidden by the achene,  
or none..... 1. *H. luteus*
- Paleae of the pappus shorter than the corolla tube—about  
half its length—not hidden by the hairs of the achene.  
A biennial with creamy white flowers..... 2. *H. tenuifolius*
- A perennial with yellow flowers; heads smaller and more  
numerous..... 3. *H. polycephalus*
2. Throat of the corolla cylindrical, 2.5-4 mm. long.  
Paleae of the pappus equalling the corolla tube, or nearly  
so.  
Throat of the corolla 2.5-3 mm. long; stem leafy..... 4. *H. arenosus*
- Throat of the corolla 3-4 mm. long; stem scapose..... 5. *H. nudatus*

### 1. HYMENOPAPPUS LUTEUS Nutt. Trans. Am. Phil. Soc. 7: 374. 1841.

Dr. Gray (Syn. Fl. N. Am. 12: 336. 1884.) made *H. luteus* a synonym of *H. filifolius* Hook., and so far as the plants of Colorado are concerned this might be all right. Some of the plants are tomentose and some are not, but they are nearly of the same size and the flowers and achenes are alike. But I hesitate to make *H. luteus* the same as the *H. filifolius* of the northwest—Oregon, Washington, and Idaho. The type locality of *H. filifolius* is the Columbia River valley, though it has been said to range from Montana through Kansas, Nebraska, and Colorado to New Mexico, but I have seen no specimens from these states and I suspect it has been confused with other species. In describing *H. cinereus* Dr. Rydberg observed: "This species has



been confused with *H. filifolius* and *H. flavescens*. . . .The species is, however, much nearer related to *H. filifolius* from which it differs mainly in the lower habit and the longer scales of the pappus." Specimens of *H. tenuifolius* have also been listed as *H. filifolius*. My collections of *H. luteus* were made from locations west of the mountains, from the vicinity of Craig in Moffat County. A part of the specimens are tomentose and a part are becoming glabrate.

2. HYMENOPAPPUS TENUIFOLIUS Pursh, Fl. 2: 742. 1814.

The type locality is "In Upper Louisiana," and the specimens were collected by Bradbury in 1810. My collections were made on the plains of eastern Colorado, where it is rather common.

3. HYMENOPAPPUS POLYCEPHALUS Osterhout, Torrey's  
18: 90. 1918.

In the Synoptical Flora (*l. c.*) under *H. filifolius* Dr. Gray wrote: "Northeastern forms are greener, more leafy, with smaller heads, approaching *H. tenuifolius*." I suspect the plants referred to are the above species, for Dr. Gray did not limit *H. filifolius* to plants with a very short pappus. This species is found along the eastern side of the foothills of northern Colorado and eastward into the Plains.

4. HYMENOPAPPUS ARENOSUS Heller, Bull. Torrey Club  
25: 200. 1898.

*H. cinereus* Rydberg, Bull. Torrey Club 27: 634. 1900.

*H. ochroleucus* Greene, Pl. Baker. 3: 30. 1901.

*H. parvulus* Greene, *l. c.*

In the original description of *H. arenosus* Heller wrote: "corollas 5 mm. long, the tube occupying nearly half the length, the throat cylindrical rather than campanulate, the triangular lanceolate lobes little more than one-fourth the length of the throat, achenes villous with long hairs; palae of the pappus oblong or slightly contracted below, a little longer than the corolla tube." Except for some less tomentum I think that *H. cinereus* Rydberg is the same, and *H. parvulus* Greene is only a small flowered, glabrate form. In some plants of *H. arenosus* the flowers may have campanulate corollas, but the long pappus scales easily

separate it from *H. tenuifolius*. The type locality of *H. arengus* is "near Espanola, Santa Fé County, New Mexico," and so far as I know, it has not been found farther north than Larimer County, Colorado. It grows both on the eastern and western sides of the mountains.

5. HYMENOPAPPUS NUDATUS Wootton & Standley,  
Contr. U. S. Nat. Herb. 16: 191. 1913.

The type locality of *H. nudatus* is in New Mexico, and a specimen of the type number is in the Rocky Mountain Herbarium of the University of Wyoming. It is probable that this is a synonym of *H. macroglottis* Rydberg (Bull. Torrey Club 27: 634. 1900.) which was somewhat doubtfully reported from Colorado in the original description.

I have two collections of *H. nudatus*, one made at DeBeque in Mesa County, the other made at Grand Junction in the same county. The Grand Junction specimen is tomentose, the other is becoming glabrate. Tomentum is not a good character by which to separate species in *Hymenopappus*.

The standing of *Hymenopappus filifolius*, as indicated above under *H. luteus*, is rather uncertain, and if it occurs in Colorado it would seem to be in the section west of the mountains where *H. luteus* is also found. The glabrate forms key as well into *H. filifolius* as into *H. luteus*.

*Hymenopappus scaposus* Rydberg (Bull. Torrey Club 27: 634. 1900.) has also been listed for Colorado, being reported by Coulter and Nelson (New Manual of Botany of the Central Rocky Mountains 555. 1909.) as ranging from Colorado to New Mexico and Nevada; but Rydberg (N. A. Flora 34: 53. 1914, and Flora of the Rocky Mountains 943. 1917.) still restricts the distribution of this species to Utah, Nevada, Arizona, and New Mexico, as at the time of its original description, and I have seen no specimens from Colorado.

WINDSOR, COLORADO



## INDEX TO AMERICAN BOTANICAL LITERATURE

1924-1925

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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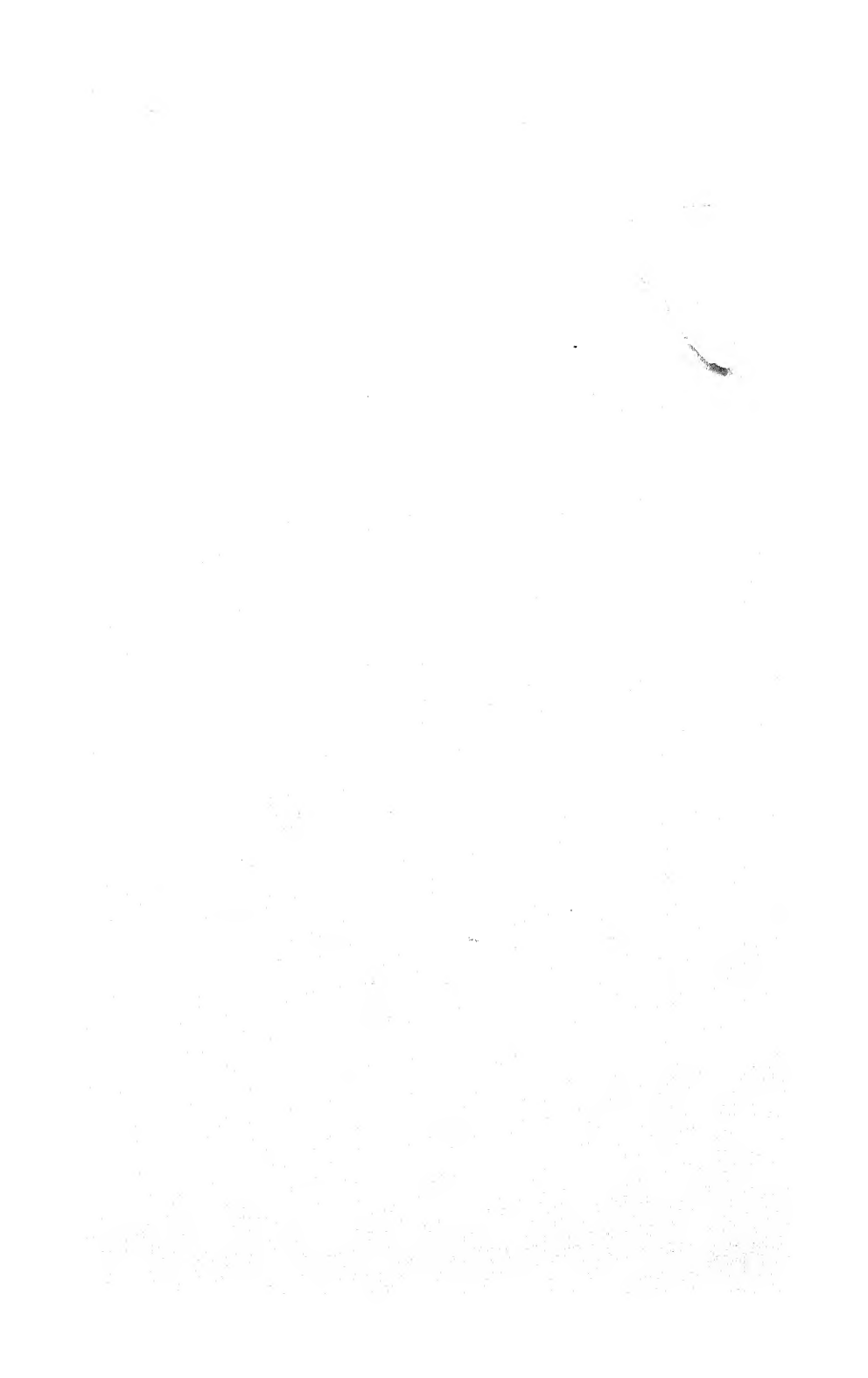
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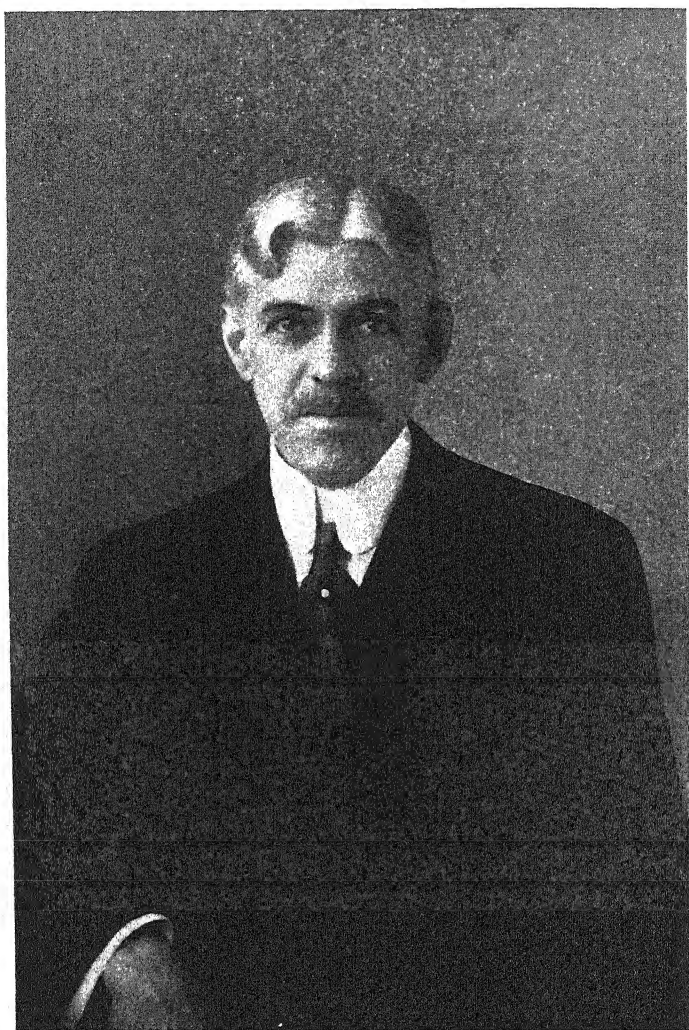
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Yours Sincerely  
G. P. Dickman

OF THE  
TORREY BOTANICAL CLUB

APRIL 1925

Eugene Pintard Bicknell  
(1859-1925)

JOHN HENDLEY BARNHART

(WITH PORTRAIT)

The death of Eugene P. Bicknell, at his home at Hewlett, Long Island, on February 9, 1925, marks the passing of one of the most careful observers among American amateur botanists. Throughout his active career, he was engaged primarily in banking, yet from the number and value of his contributions to botanical literature one might reasonably have inferred that he was by profession a scientific worker.

Eugene Pintard Bicknell was born September 23, 1859, at Riverdale-on-Hudson, then in Westchester County but long since swallowed up by the expansion of the City of New York. Through his father, Joseph Inglis Bicknell, he was descended from Zachary Bicknell, who settled at Weymouth, Massachusetts, in 1635, and from Gregory Dexter, who settled in Rhode Island in 1643 and was president of Providence and Warwick in 1653-54. His paternal grandmother, Emeline Valeria Pintard Inglis of Philadelphia, came from the old Pintard family of Monmouth County, New Jersey, whose progenitor, Anthony Pintard the Huguenot settler of 1691, was a benefactor of the old French Church of New York. Through his mother, Maria Theresa Pierrepont, he was descended from Sir Robert de Pierrepont, who fought at the battle of Hastings in 1066, and Rev. James Pierpont, who was more than any other man actively concerned in the establishment of Yale College. He was also related to the Jay, McVicar, and other well-known old New York families, and was a member of various patriotic societies, such



as the St. Nicholas Society, the Huguenot Society, the Sons of the Revolution, and the Society of Colonial Wars.

He was a very modest man, always reticent concerning himself, and the writer, although enjoying his acquaintance for more than thirty years, is not well informed concerning the details of his life-history. He was not a college graduate, yet it is evident from his early scientific papers, published several years before he attained his majority, that his education was a thorough one. He was long connected with the firm of John Munroe & Company, foreign bankers of New York City, and was eventually a partner in that firm as well as the affiliated Munroe & Cie., of Paris. After many years of bachelorhood, he married Edith Babcock, at Riverdale-on-Hudson, October 9, 1901, and they had two daughters, Eleanor Franklin, who, after two years with the class of 1926 at Vassar College, gave up her course to be with her father but has been transferred to Teachers College, Columbia University, and Edith Evelyn, a freshman at Vassar. His home had always been at Riverdale, but soon after his marriage he settled in southwestern Nassau County, where he lived the rest of his life.

But it is with his career as a scientist that we are chiefly concerned. His interest in birds and flowers began early, and he was then more ornithologist than botanist. His first technical published paper was on "Evidences of the Carolinian fauna in the lower Hudson Valley." This was published in the Bulletin of the Nuttall Ornithological Club in 1878, when he was only eighteen years old, and was followed by several others before his first contribution to botanical literature. In the same year, 1878, he was one of the group of ten naturalists who organized the Linnaean Society of New York, and he was the president of this society from 1879 to 1887. It was during his presidency that this society published its two volumes of Transactions, and in the first of these appeared one of the most important of his earlier scientific papers, "A review of the summer birds of a part of the Catskill Mountains, with prefatory remarks on the faunal and floral features of the region." While this was based chiefly upon his own observations, he also made use of the notes of others, among these being his brothers Pierrepont Constable Bicknell and George Augustus Bicknell. He was one of the founders, and a life fellow, of the American Ornithologists' Union.

It was at the meeting of January 13, 1880, that Eugene P. Bicknell was elected to membership in the Torrey Botanical Club, and in the club's Bulletin for May of that year appeared his first botanical papers. These were the first of fifty-seven contributions from his pen to the pages of the Bulletin of the Torrey Botanical Club, the last in 1919.

In 1894, students of the local flora of the vicinity of New York were startled by a paper in the Bulletin, which called attention to the fact that there were two species of *Helianthemum* in this region, both well known but always hitherto confused with each other. This was followed in quick succession during the two following years by others on *Sanicula*, *Sisyrinchium*, *Scrophularia*, and *Agrimonia*. Local botanists began to rub their eyes, and wonder whether they were themselves blind, or Bicknell was possessed of abnormally acute vision. His descriptions were so clear that it was easy for anyone else to convince himself of the accuracy of the newly-published observations, and the reputation of E. P. Bicknell was securely established as one of the most discriminating of observers.

His interest in *Sisyrinchium* led him to careful study of material from all parts of the United States, resulting in a series of ten papers devoted to this genus. Later he became particularly interested in the flora of the island of Nantucket, which he had visited in 1889 and 1899, and where he spent as much of his time as he could spare from business from 1904 to 1912. This resulted in a flora of Nantucket, printed in the Bulletin of the Torrey Botanical Club in twenty instalments from 1908 to 1919. This flora contains, incidentally, his principal published references to his earlier collections at York Harbor and Mount Desert, Maine.

In 1896, he became an annual member of the newly organized New York Botanical Garden, his name appearing in the first printed list; and in the same year he was elected a corresponding member of the Philadelphia Botanical Club, organized five years earlier. He was a member of the corporation of The New York Botanical Garden from 1910 until his death, and a member of the board of scientific directors from April 24, 1913, to January 8, 1923, when his resignation on account of ill-health was accepted by the board of managers. His last contribution to botanical literature seems to have been the text accompanying the plate

(no. 205) of *Hypopitys insignata* in Addisonia, in 1921. Although his health had been failing for several years, news of his death came as a surprise to his botanical friends.

The accompanying portrait is from a photograph taken in December, 1910. The appended bibliography is believed to be nearly or quite complete. Mrs. Bicknell has presented her husband's extensive plant collections and botanical books to the New York Botanical Garden.

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Also as a separate.

The ferns and flowering plants of Nantucket.—IV. Bull. Torrey Club 36: 1-29. 29 Ja 1909.

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Also as a separate.

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Also as a separate.

The ferns and flowering plants of Nantucket—X. Bull. Torrey Club 39: 415-428. 9 S 1912.

Also as a separate.

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Also as a separate.

The ferns and flowering plants of Nantucket—XVI. Bull. Torrey Club **42**: 549-570. 13 N 1915.

Also as a separate.

The ferns and flowering plants of Nantucket—XVII. Bull. Torrey Club **43**: 265-276. 16 Je 1916.

Also as a separate.

*Pinus Banksiana* on Nantucket. Rhodora **18**: 241, 242. 1 D 1916.

The Acadian chickadee on Long Island. Auk **34**: 91, 92. 2 Ja 1917.

*Baccharis halimifolia*. Addisonia **2**: 29, 30. pl. 55. 30 Je 1917.

The ferns and flowering plants of Nantucket—XVIII. Bull. Torrey Club **44**: 369-387. 10 Au 1917.

Also as a separate.

Late southward migration of the Cape May warbler on Long Island. Auk **34**: 483, 484. 10 O 1917.

*Aster cordifolius*. Addisonia **2**: 79, 80. pl. 80. 31 D 1917.

The ferns and flowering plants of Nantucket—XIX. Bull. Torrey Club **45**: 365-383. 20 S 1918.

Also as a separate.

*Aster laevis*. Addisonia **3**: 47, 48. pl. 104. 30 S 1918.

*Ilex verticillata*. Addisonia **3**: 71, 72. pl. 116. 31 D 1918.

The short-eared owl breeding on Nantucket. Auk **36**: 284, 285. 8 Ap 1919.

The ferns and flowering plants of Nantucket—XX. Bull. Torrey Club **46**: 423-440. 8 D 1919.

Also as a separate.

*Hypopitys insignata*. Addisonia **6**: 25, 26. pl. 205. 15 S 1921.

The status of the black gyrfalcon as a Long Island bird. Auk **41**: 64-68. 10 Ja 1924.

## Botrychium lanuginosum and its relation to the problem of the fertile spike

M. A. CHRYSLER

(WITH PLATE 4)

In an earlier paper (3) the writer discussed the morphological nature of the fertile spike in the Ophioglossaceae, and reached the conclusion that the evidence at hand supported one of the suggestions of Roeper (6) to the effect that the fertile spike represents two fused pinnae, namely the basal ones of the leaf, the rest of the pinnae being sterile. The evidence advanced by the writer to support this view indicated that the vascular supply of the fertile spike of *Botrychium* arises precisely like that of any pair of the sterile leaflets. Additional evidence was furnished by certain abnormal specimens of *B. obliquum* Muhl. which showed two or more fertile spikes; the vascular supply of the spikes in these specimens was found to be in accord with the theory of Roeper.

The writer's excuse for reopening the discussion at this time is the "discovery" of a number of herbarium sheets of a species of *Botrychium* which appears to have been overlooked but which offers very definite evidence on the question of the nature of the fertile spike in the genus under consideration. This species is *B. lanuginosum* Wall. (at one time not separated from *B. virginianum*), a plant occurring in southeastern Asia, generally at high altitudes. Although the species takes its name from the "lanugo" or long silky hairs which scantily cover the leaves, the most striking feature is the position of the sporogenous portion. While this plant is undoubtedly a *Botrychium*, most specimens do not show what could properly be called a fertile spike, but present the appearance of having the second, third or higher leaflet function as the fertile or sporogenous organ. Twenty-four specimens have been examined, through the kindness of the curators of the Gray Herbarium, Missouri Botanical Garden, New York Botanical Garden, and United States National Herbarium, and in these specimens the fertile part occupies the position of the second, third, fourth, fifth, or sixth leaflet, with a decided preponderance in the class of the third leaflet. FIG. 1,



from a specimen kindly loaned by the Curator of the Herbarium of the Missouri Botanical Garden, clearly shows the fertile part occupying the position of the third leaflet. Although in this specimen the leaflets are disposed alternately, cases are not lacking where most of the leaflets are opposite, as is shown in FIG. 2, a photograph of sheet 776,951 of the National Herbarium. This interesting specimen has leaflets 1 and 2 opposite, 3 and 4 opposite, then the fertile spike which here appears to represent two fused leaflets, followed by sterile leaflets arranged in pairs for the most part.

Through the marked kindness of the Curator of the Gray Herbarium, a specimen closely resembling the one just described has been available for microscopic study. The critical region of the leaf has been swelled out by means of hot dilute ammonia, imbedded in paraffin and made into serial sections. From these it is perfectly clear (1) that the fertile spike has a double vascular supply, in contrast to the single vascular supply of the sterile leaflets, and (2) that each half of the vascular supply of the fertile spike is attached to the leaf trace of the rachis exactly as is the single trace from each sterile pinna, and precisely as has been described by the writer for *B. virginianum* (3, p. 3), that is, each pinna trace joins the C-shaped trace of the rachis near one edge of the latter, subtending a narrow pinna-gap. This condition has been shown (*l.c.*) to correspond to what may be seen in the leaves of such primitive ferns as *Osmunda* and *Todea*. It is safe to conclude that the fertile spike of the specimen represented in FIG. 2 consists likewise of two fused pinnae. Although no material of plants like FIG. 1 has been available for sectioning, it may be confidently predicted that the fertile spike of such cases will show a single trace attached to the trace of the rachis in the same manner as is the trace of a sterile pinna.

It is obvious that *B. lanuginosum* is a very variable species. According to Bitter (1, p. 471) it is perhaps second only to *B. Lunaria* in this respect, showing variability not only in size, in position of the fertile spike and in arrangement of the pinnae, but also in the not infrequent occurrence of a second smaller fertile spike farther up on the leaf than the first spike. This feature is not represented in the specimens to which I have had access, but is realized in a specimen of *B. ramosum* (Roth.) Aschers., represented in FIG. 3, collected at Fairlee, Vermont, by Dr. H. M.

Denslow and deposited in the Herbarium of the Brooklyn Botanic Garden, the Director of which institution has kindly furnished the photograph. This specimen not only shows an extra pair of fertile spikes, but displays a forking of the large fertile spike which reminds one of the cases already described by the author (3) in which the fertile spike of *B. obliquum* is either forked or else divided all the way to the base. Reference may also be made to *figure 25* of the author's earlier paper (3), showing one of the pinnae of *B. obliquum* developed as a fertile organ, a condition which has been observed in several species and is figured for *B. Lunaria* by Goebel (5). Another variable feature of *B. lanuginosum* mentioned by Bitter (*l.c.*) is the not infrequent occurrence of a few sporangia on the edges of sterile leaflets, a condition also observed by Goebel (5) in *B. Lunaria*.

The genus *Aneimia* has already been referred to as a case where the two basal pinnae of each leaf are specialized as the spore-bearing part and turn sharply upward (see *fig. 23* of 3). It is interesting to note that in this genus there are species where a single fertile spike or leaflet takes the place of the usual pair. The herbarium of the New York Botanical Garden contains six specimens of a plant labelled "*Ornithopteris* sp. nov., Santa Marta, U. S. of Colombia, col. Herbert H. Smith 1898-9." In each of these specimens a single fertile spike arises at the base of the green region of the leaf, apparently in the adaxial position, after the manner of a typical *Botrychium*. The same condition is shown by *Aneimia Wrightii* Baker, a rare little fern collected by the indefatigable Wright in eastern Cuba in 1859-60. Whether the fertile spike in these cases represents a single pinna or a fusion of two basal pinnae is not possible to make out from the herbarium sheets, but the general resemblance to what seems to have happened in *Bctrychium* is exceedingly suggestive.

In attempting to fit the Botrychiums into their place it may be well to recall that, beginning with the generalized type of fern leaf in which each leaf bears spores on all of its branches, localization of the area of spore-production in fern leaves has proceeded in two ways:

(1) The leaves of the current season show a greater or less differentiation into vegetative and reproductive organs. This method of effecting division of labor, the so-called heterophylly, shows many gradations and is widespread. Familiar examples

are *Lorinseria areolata* (L.) Underw. (= *Woodwardia angustifolia* Sm.), *Struthiopteris germanica* Willd., and *Osmunda cinnamomea* L.

(2) The differentiation appears in individual leaves—

(a) Only the tip region is fertile, e. g., *Polystichum acrostichoides* (Michx.) Scott, *Osmunda regalis* L.

(b) Only the median region is fertile, e.g., *Osmunda Claytoniana* L., *Botrychium lanuginosum* Wall.

(c) Only the basal region is fertile, e.g., *Aneimia* spp. In this genus the fertile pinnae are raised into a favorable position. Most species of *Botrychium* appear to belong in this class, and show the specialization carried to a high degree by fusion of the two basal pinnae as well as by being raised into an erect position.

That the genus *Botrychium* is a highly specialized one is indicated by certain features which have been reported for *B. virginianum*: a well marked cambium in the stem, the symbiotic subterranean gametophyte, the production of only one (or two) leaves per season, with the primordia of others early laid down. At the same time there is foundation for the view that the family has branched off from the main fern stock at a comparatively low level; this appears to be the mature judgment of Bower (2, p. 294) who suggests Osmundaceae and Botryopterideae as the probable nearest relatives.

On account of the generalized and plastic nature of *Botrychium lanuginosum*, as brought out in the foregoing account, it may be suggested that in this species we see more nearly than in the other species what the ancestral *Botrychium* looked like, namely, a fern in whose leaf spore production was restricted to one or two pinnae occupying no special region of the leaf (FIG. 1). Individuals occurred in which the leaflets were opposite rather than alternate; two opposite fertile leaflets became fused (FIG. 2). Finally the location of the fertile leaflets became fixed at the level of the basal pair (seen in the closely related *B. virginianum*).

The uncovering of *B. lanuginosum* provides exactly the sort of evidence which was lacking at the time of the writer's earlier studies on Ophioglossaceae; this species almost constitutes a living fossil *Botrychium*, much as the megasporophyll of *Cycas revoluta* has been styled a living fossil cycad. There now appears to be no reasonable doubt that the fertile spike of the common species of *Botrychium* represents a fused pair of pinnae, namely

the basal pair. Such a view of course precludes the possibility of a strobilar origin of the aerial organ of Ophioglossaceae. In fact the opinion may be ventured that if Bower had been acquainted with *B. lanuginosum* he would scarcely have advanced the theory of a strobilar origin for the group, a view which he has relinquished (2) upon the basis of evidence derived from all aspects of the question. Moreover, upon the basis of the accumulated evidence, there would seem to be no more reason for retaining the order Ophioglossales than for framing an order for the Osmundaceae; in other words, the family Ophioglossaceae should be placed in Filicales rather than in a separate order.

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#### Description of plate 4

FIG. 1. *Botrychium lanuginosum* Wall., from sheet no. 1602 of the Missouri Botanical Garden (reduced).

FIG. 2. *Botrychium* (species not assigned, but probably *B. lanuginosum*) from sheet no. 776,951 of the U. S. National Herbarium.

FIG. 3. *Botrychium ramosum* (Roth) Aschers., abnormal specimen in the herbarium of the Brooklyn Botanic Garden.



CHRYSLER ON BOTRYCHUM LANUGINOSUM



## Contributions to the flora of Long Island, New York Third paper\*

WILLIAM C. FERGUSON

The plants listed below represent species that, in the writer's experience, are from uncommon to, in some instances, very rare, and were all collected during the season of 1924 while on solitary rambles, with the following exceptions: *Poa bulbosa* was found by Mr. Hal Fullerton of Medford, L. I.; *Carex leucorum*, by the late Mr. Eugene P. Bicknell; *Triosteum aurantiacum*, by Mrs. Asa Wells of Riverhead, L. I.; *Rhynchospora cymosa* and *Aster paniculatus*, while with Mr. Norman Taylor of the Brooklyn Botanic Garden.

With the exception of *Fimbristylis puberula*, *Juncus brachycarpus*, *Drymocallis agrimonioides*, *Hottonia inflata*, *Bartonia paniculata*, *Menyanthes trifoliata*, and *Aster acuminatus*, as to the identity of which the writer felt certain, all names were confirmed or corrected by the following authorities:

Grasses by Mrs. Agnes Chase.

Sedges, except *Carex*, by Dr. N. L. Britton.

*Carex*, except the Montanæ group, by Mr. Kenneth K. Mackenzie.

*Carex*, Montanæ group, by Mr. Eugene P. Bicknell.

*Cuscuta* by Professor T. G. Yuncker.

*Aster* by Professor Edward S. Burgess.

All others by Dr. J. K. Small, Dr. F. W. Pennell, Professor M. L. Fernald, and Mr. C. A. Weatherby, whose names appear in the text, and to all of whom I wish here to express grateful acknowledgement.

POA BULBOSA L. Riverhead: waste ground. Introduced from Europe.

CHAETOCHELOA GENICULATA (Lam.) Millspaugh & Chase, Field Mus. Publ.

Bot. 3: 37. 1903. Millneck; Merrick; Montauk: salt marshes and bordering meadows. (This is *C. imberbis* of Britton's Manual.)

SCLERIA TRIGLOMERATA Michx. Central Islip: pine barren swamps.

FIMBRISTYLIS PUBERULA (Michx.) Vahl. Hempstead: damp meadow.

RHYNCHOSPORA CYMOSA Ell. Montauk: swampy meadow. The writer can find no previous record for Long Island.

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\* The previous papers of this series appeared in *Torreya* 22: 43-49. 1922, and in *Bull. Torrey Club* 51: 177-201. 1924.



*SCIRPUS NANUS* Spreng. Massapequa: soft mud in salt marsh. Montauk: soft mud shore of Oyster Pond, brackish.

*SCIRPUS PLANIFOLIUS* Muhl. Wyandanch; Kings Park; Kew Gardens; Deer Park; Port Washington: all localities in dry or rich hilly woods.

? *SCIRPUS PALUDOSUS* A. Nelson.

The writer cannot separate these small plants with dense, compact inflorescence and growing singly or but few together, from the larger *Scirpus robustus* which grows in dense masses with stout rootstocks. Measurement of the achenes and of the awns on the scales shows no material difference between the two, and Dr. N. L. Britton, to whom the writer has shown the smaller plants, has named them all *S. robustus*. The writer is inclined to believe that these smaller plants are seedlings or, at least, much younger plants than the larger typical specimens of *Scirpus robustus*. If this could be demonstrated, these smaller plants would not even be entitled to varietal rank. These smaller plants are from one to two feet tall. The writer has seen large colonies of *S. robustus* six feet tall or more. It takes time for rootstocks to grow to the size represented in these colonies. It is to be hoped that other botanists will study this subject in the field.

*CAREX ABDITA* Bicknell, Bull. Torrey Club 35: 491-2. 1908. Wyandanch; Kings Park; Richmond Hill; Kew Gardens: all in rich or dry hilly woods. Merrick: thicket edge, salt marsh.

*CAREX ROSEA* Schk. Woodside: very swampy rich woods.

*CAREX MITCHELLIANA* M. A. Curtis. (See C. A. Weatherby, *Rhodora* 25: 17. 1923.) East Moriches: open bog. Montauk: bog near Oyster Pond. Millneck: boggy woods.

*CAREX STRIATULA* Michx. Queens: rich hilly woods.

*CAREX MESOCHOREA* Mackenzie, Bull. Torrey Club 37: 246. 1910. (*C. mediterranea* Mackenzie, Bull. Torrey Club 33: 441. 1906.) Garden City: grassy village roadside, introduced from further south.

*CAREX TRIBULOIDES SANGAMONENSIS* Clokey, *Rhodora* 21: 84. 1919. Queens: swamp in hilly rich woods.

*CAREX LEUCORUM* Willd. Enum. Pl. Berol. Suppl. 63. 1809. (Name only.) Enum. Pl. Berol. (ed. 2) 2: 380. 1822. The earliest application of a varietal name to the plant is *Carex pennsylvanica distans* Peck, Rept. N. Y. State Mus. 46: 131. 1893.

Valley Stream: border of dry sandy level woods.

*CAREX RUGOSPERMA* Mackenzie, Bull. Torrey Club 42: 621. 1915. Kew Gardens: hilly rich woods.

*CAREX LAXICULMIS* Schwein. X *C. ABSCONDITA* Mackenzie. Millneck: swampy hilly woods.

*CAREX VARIA* Muhl. X *C. UMBELLATA* Schk. Kings Park: dry hilly oak woods.

*CAREX ABSCONDITA* Mackenzie, Bull. Torrey Club 37: 244. 1910. (*C. ptychocarpa* of the manuals.) Last year the writer had observed that the swollen distorted perigynia, so characteristic of this species here on Long Island, contained achenes that were oblong, longer and narrower than are the normal achenes, and that these abnormal ones were all split and empty. This season in further investigation of the cause he found a live grub that about completely filled the achene.

JUNCUS BRACHYCARPUS Engelm. Freeport: open bog. The writer can find no previous record for Long Island.

IBIDUM VERNALE (Engelm. & Gray) House. Merrick: elevation on salt marsh. Determination by Dr. H. M. Denslow.

SALIX VIMINALIS L. Merrick: border of swamp and old clearing. Native of Europe.

POLYGONUM PROLIFICUM (Small) Robinson. Merrick; Massapequa; Amityville; Oyster Bay: all in salt marshes.

POLYGONUM ATLANTICUM (Robinson) Bicknell.

The writer has found a plant with achenes as in *P. atlanticum* and also exerted achenes of various lengths and believes *P. exsertum* Small to be a viviparous condition of *P. atlanticum*. Witmer Stone and Eugene P. Bicknell have published similar opinions.\*

SAGINA APETALA Ard. Wading River: shady village roadside.

SAGINA DECUMBENS (Ell.) T. & G. Garden City: shady village roadside.

SAGINA PROCUMBENS L. Montauk: brackish wet shore of Oyster Pond.

Plants densely tufted. Determinations of *Sagina* by J. K. Small.

ARABIS LYRATA L. Oyster Bay: damp open hillsides.

CARDAMINE HIRSUTA L. Roslyn: damp open hillside.

DRYMOCALLIS AGRIMONIODES (Pursh) Rydb. Meadowbrook: dry gravelly bank.

ERODIUM CICUTARIUM (L.) L'Her. Babylon: grassy field; adventive from Europe.

GERANIUM MOLLE L. Setauket: waste field; adventive from Europe.

VITIS BICOLOR LeConte. Riverhead: roadside thicket.

HOTTONIA INFLATA Ell. Riverhead: small pond on Sound Avenue. Mr. E. S. Miller directed the writer to this locality where he had collected it fifty years ago. Mr. E. P. Bicknell has written the writer that it grows at Hewlett, Long Island.

BARTONIA PANICULATA (Michx.) Robinson. North of Good Ground, in sphagnum in coast cedar swamp.

MENYANTHES TRIFOLIATA L. Water Mill: open swamp. Mr. F. S. Benedict directed the writer to this locality and plant.

CUSCUTA CORYLI Englm. Middle Island: pine barren swamp.

CUSCUTA COMPACTA Juss. Millneck; Massapequa: thicket edge of swampy woods. Queens: rich hilly woods. Merrick: swampy low woods. Southold: open swampy meadow.

CUSCUTA GRONOVII LATIFOLIA Engelm. Southold: open swamp.

CUSCUTA GRONOVII VULGIVAGA Engelm. Millneck: swampy thicket. Massapequa: swamp woods. Merrick: salt marsh. Hempstead: garden.

SCUTELLARIA INTEGRIFOLIA L. Massapequa: damp meadow near salt marsh. Wyandanch: dry hilly woods.

SOLANUM VILLOSUM (L.) Mill. Montauk: sandy shore of brackish Oyster Pond. Point O Woods: ocean sand dunes.

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\* Witmer Stone. Plants of southern New Jersey. Rep. N. J. State Mus. 1910: 425. Eugene P. Bicknell. Flora of Nantucket. Bull. Torrey Club 36: 450. 1909.

GRATIOLA AUREA forma leucantha Bartlett, Rhodora 9: 123. 1907. (Flowers white). Sweezytown: shore of small pond. Determined by F. W. Pennell who had no record from our area when he revised *Scrophulariaceae*, and who had never seen it growing. Obviously very rare.

TRIOSTEUM AURANTIACUM Bicknell. Sound Avenue, Riverhead: damp thicket.

LACTUCA FLORIDANA (L.) Gaertn. Port Washington: rich, hilly woods.

HIERACIUM VULGATUM Fries. Oakdale: roadside and fields.

EUPATORIUM ALBUM L. Middle Island: border of pine barren swamp.

SOLIDAGO HISPIDA Muhl. Montauk: hither woods. One colony on dry hilly oak woods growing with *Solidago bicolor*. Comparatively few plants and averaging lower and slenderer than associated *S. bicolor*. The writer can find no previous record for Long Island.

SOLIDAGO RUGOSA SPHAGNOPHILA Graves.

SOLIDAGO ULMIFOLIA Muhl.

In hilly rich woods at Queens the writer found plants that he could not satisfactorily place with either glabrate forms of *S. rugosa*, or with *S. ulmifolia*, and sent them to Professor M. L. Fernald, who with Mr. C. A. Weatherby at the Gray Herbarium, determined them as probably hybrids or intermediate forms of *Solidago ulmifolia* Muhl. and *Solidago rugosa sphagnophila* Graves.

ASTER ACUMINATUS Michx. Montauk: hilly rich woods.

ASTER IANTHINUS Burgess. In Gray's Manual, 7th ed. (p. 805), this species, with the two following included as synonyms, is made a variety of *Aster macrophyllus* L. Plattsdale: hilly rich woods. Massapequa: dry level oak woods.

ASTER MULTIFORMIS Burgess. Plattsdale: hilly rich woods.

ASTER VIOLARIS Burgess. Hempstead Reservoir: bank oak woods.

ASTER MACROPHYLLUS L. Millneck: hilly rich woods.

ASTER SCHREBERI Nees. Plattsdale: hilly rich woods.

ASTER SAGITTIFOLIUS Willd. Douglaston: hilly rich woods.

ASTER SAGITTIFOLIUS DISSITIFLORUS Burgess. Douglaston: hilly woods.

The writer can find no previous record of *A. sagittifolius* for Long Island.

ASTER TARDIFLORUS L. (*A. patulus* Lam). Millneck: hilly rich woods; single plant. Dr. Burgess is inclined to believe from field experience that this *Aster* is a hybrid.

Intermediate forms between *A. paniculatus* and *A. salicifolius*, *A. paniculatus* and *A. Tradescanti*, *A. salicifolius* and *A. Tradescanti*, *A. Tradescanti* and *A. vimineus*, *A. Tradescanti* and *A. lateriflorus*, *A. lateriflorus* and *A. vimineus*, are not uncommon on Long Island. The writer this season has found all of these forms. His determinations have been verified or corrected by Dr. E. S. Burgess.

## Chomelia, Jacquin and Anisomeris, Presl

H. H. RUSBY

(WITH TWO TEXT-FIGURES)

The genus *Chomelia* of the Rubiaceae was founded by Jacquin on *C. spinosa* (Select. Stirp. Amer. Hist. 18. pl. 13. 1763). The genus *Anisomeris* was founded by Presl on *A. spinosa* (Symb. Bot. 2: 5. pl. 54. 1833). Subsequent authors, assuming erroneously that the two genera were identical, have concerned themselves with the question as to which name is correct. The name *Chomelia* had been used by Linné in 1737, in a different connection, hence some authors hold that Jacquin's name is untenable, and Otto Kuntze (Rev. Gen. Pl. 1: 277. 1891) proposed *Caruelina* to replace it, rejecting *Anisomeris*, apparently because there was an *Anisomera*. Under rules now generally accepted, both of these objections fail, since Linné abandoned his name *Chomelia* in 1753, and no other author appears to have used it between that date and the time of its proposal by Jacquin. This leaves Jacquin's name to stand for all species having the generic characters pertaining to *C. spinosa*. Both of the essential characters of this genus are perfectly displayed in Jacquin's picture, though scarcely referred to in his description. They are (1) the possession of dorsal horns or awns by the corolla-lobes; (2) a characteristically sagittate anther. In all the species of which I have been able to examine specimens or figures, these two characters are associated, or both are wanting. The study of descriptions is of little avail, as nearly all authors have either overlooked or ignored these characters, which are not referred to in their descriptions. The present article, therefore, can enumerate only the few species whose characters I have thus been able to establish.

There is not the slightest difficulty in determining the affinity of any species if a well-developed bud can be seen, as the four corolla-lobes of *Chomelia* are concave, usually with their tips inflexed, and bear vertical, mostly hollow awns or horns, which stand free and separate, as a sort of crown to the bud. Some authors have described these lobes as "acuminate," but they are not really so. In fact, I have seen no member of either

genus that has acuminate corolla-lobes. It is the dorsal horns which have been mistaken for terminal acuminations. The slightest manifestations of these horns that I have seen is in *C. Pohliana* Muell.-Arg., figured in Martius' Flora of Brazil. In this species, they are mere hollow conical protuberances at the end of the bud. In the next succeeding plate (*C. ribesoides* Muell.-Arg.) there is no trace of such appendages, and it seems strange that this character should have been overlooked at that time. It appears still more strange that it should have been overlooked in Jacquin's figure, which shows almost the extreme degree of development of these awns.

In one or two species, the tip of the corolla-lobe is almost obsolete, so that the appendage is almost continuous with the end of the lobe.

The difference in the anthers is quite as striking. Jacquin's figure shows strongly sagittate anthers, with the basal lobes acuminate. In some species this acumination is extreme, reaching the state of attenuation. Presl's figure of *Anisomeris* does not show the anthers, but I have examined enough species to show that, with naked corolla-lobes, there is always an anther with the thecae parallel and contiguous to their short, obtuse bases.

The species of the two genera, so far as I have been able to determine them, are as follows:

#### CHOMELIA Jacquin

1. *C. SPINOSA* Jacq. Select. Stirp. Amer. Hist. 18. pl. 13. 1763.
2. *C. POHLIANA* Muell.-Arg. Flora 58: 452. 1875. (*Anisomeris Pohliana* Chodat & Hassl. Bull. Herb. Boiss. II. 4: 175. 1904.)
3. *C. Purpusii* (Brandege) n. comb. (*Anisomeris Purpusii* Brandege, Univ. Calif. Publ. Bot. 6: 70. 1914.)

Gleason's no. 295, from "dense upland forest, Tumatumari, British Guiana," is said by N. E. Browne to be "near *C. tenuiflora* Benth.," to which species Standley refers it. Gleason's plant is a *Chomelia*, with the corolla-appendages stout, brown and indurated and with the basal lobes of the anthers rather short, the anthers projecting beyond the mouth of the corolla.

The following species appear not to have been published:

4. *Chomelia longicaudata* n. sp. (*C. brachyloba* Standley, Contr. U. S. Nat. Herb. 18: 136, in part. 1916.) Pilose with mostly appressed gray hairs. Branchlets short, slender, crowded, leafy. Stipules 3 to 5 mm. long, setaceous, acute. Petioles 5 to 7 mm. long. Blades 3 to 7 cm. long, 2 to 3 cm. broad, oval and somewhat rhomboidal, abruptly contracted at both ends, especially at the base, acute, entire, thin, drying brownish, the upper surface sparsely strigose, the lower densely so, with midrib and secondaries sharply prominent, the secondaries 8 or 10 on a side, strongly falcate-ascending. Peduncles axillary, mostly solitary, slender, about 2 cm. long, slightly thickened toward the summit, where the sessile flowers are crowded in a cyme that is

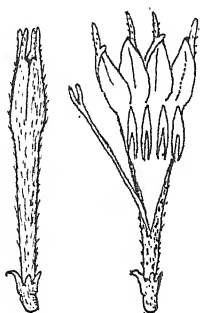


FIG. 1. ( $\times 2$ )  
*C. longicaudata*.



FIG. 2. ( $\times 2$ )  
*C. brevicornu*.

usually shortly bifid. Bud densely white-strigose, the horns conspicuous. Calyx-tube infundibular, about 2 mm. long, the limb campanulate, short, purplish, the teeth thick and rigid, somewhat spreading, acute, unequal, the longest 1.25 mm. long. Corolla tube 12 to 15 mm. long, very slender, slightly broadened toward the summit. Lobes widely spreading, oval, 3 or 4 mm. long, exclusive of the horn, which is sometimes a third as long, slender. Anthers attached at the summit of the tube, extending beyond the base of the lobes, sessile, sagittate, the lobes acuminate, about as long as the body. Style exserted, the lobes oblong, nearly 1 mm. long. FIG. 1.

Standley's *C. brachyloba* is based on Pittier's Central American specimen, which is an *Anisomeris*, and is transferred to this genus below, this leaving Smith's *Chomelia* without a name, unless we were to hold that the specific name *brachyloba* must apply to both species, in the different genera. This seems untenable, and tending to confusion. Smith's no. 392, therefore, collected near Santa Marta, Colombia, 1898-1899, and deposited in the her-

barium of the New York Botanical Garden, is made the type of *C. longicaudata*.

5. *Chomelia brevicornu* n. sp. Coarsely short-pilose with gray hairs. Branchlets elongated, rather slender, gray, terete. Spines axillary or slightly supra-axillary, stout, pungent, gray, 1 to 2 cm. long. Stipules 8 to 10 mm. long, broadly triangular, acuminate and acute, pilose. Petioles 1 to 2 cm. long, broad. Blades to 8 or 9 cm. long and 4 cm. broad, very unequal, ovate, abruptly acuminate and acute at both ends, entire, drying brown, nearly glabrous above, except on the principal veins, which are lightly ferruginous-hairy and lightly impressed, more hairy beneath, where the midrib and secondaries are strong and prominent, the latter about 8 or 10 on each side, strongly ascending and lightly curved, the venation very finely and lightly anastomosing. Cymes long-peduncled, densely flowered at the summit, the flowers sessile. Bractlets about equalling the calyx, thick and rigid, obtuse. Calyx-tube cylindrical, 1.5 mm. long, 1 mm. thick, a little shorter than the limb, which is deeply divided, the 4 teeth thick and rigid, somewhat recurved, obtusish. Corolla nearly 2 cm. long, the teeth 4 or 5 mm. long, oblong, obtuse, the dorsal awn short, stout and rigid, dark colored. Anthers linear, nearly 3 mm. long, extending to the base of the corolla-lobes, attached at about the middle of the back. Style filiform, exceeding the anthers, the stigmas nearly 1 mm. long, erect, obtuse, oblong. FIG. 2.

Type collected by the author at Rurrenabaque, Prov. Beni, Bolivia, altitude 1000 feet, October 15, 1921 (Mulford Explor. no. 1282) and deposited in the herbarium of the New York Botanical Garden.

"A small tree with white flowers, in second growth of forest."

6. *Chomelia dimorpha* n. sp. Young portions, veins of the lower leaf surfaces etc., appressed pubescent. Branchlets slender and weak, gray. Spines short, gray. Stipules nearly 1 cm. long, 2 mm. wide, lanceolate with attenuate summit, broadly keeled. Petioles 3 to 5 mm. long, stout. Blades up to 1 dm. long and 4 cm. broad, ovate, with obtuse base and acuminate and acute summit, entire, thin, nearly glabrous above, the pubescent reddish midrib and secondaries sharply prominent beneath, the latter about 12 on a side, strongly ascending. Cymes axillary, mostly solitary, shortly peduncled, densely flowered, the flowers of two kinds. Calyx of the normal flowers 2.5 mm. long, urceolate-campanulate, the teeth little more than a fourth of the length, sub-equal, nearly erect, acute. Corolla-tube 6 mm. long, regularly cylindrical, the limb 5 mm. long, divided nearly to the base, the tips of the lobes nearly obsolete, the appendages obtusish. Anthers 2 mm. long, very slender,

acuminate, extending a little beyond the base of the corolla-lobes, the attenuate basal lobes about a third of the length. Stigmas reaching beyond the middle of the corolla-lobes, erect, linear-oblong, nearly as long as the anthers.

Associated with these flowers are a few with corollas only 2 or 3 mm. long, the lobes as long as the tube, the anthers stouter and better developed, and the flowers apparently quite perfect.

Type collected by O. Buchtien (*no.* 206) at Coroico, Yungas, Prov. La Paz, Bolivia, altitude 1100 meters, Oct. and Nov. 1912, and deposited in the herbarium of the New York Botanical Garden.

Species very near *C. brevicornu*, but distinguished by the character of the branchlets, the indumentum and inflorescence.

7. ***Chomelia multiflora*** n. sp. Densely and softly pubescent with short, spreading gray hairs. Spines long and slender, very pungent. Flowering branchlets numerous, short. Stipules not seen. Petioles to 5 mm. long, mostly almost obsolete. Blades crowded on the short branchlets, to 5 cm. long and 3 cm. wide, oval, verging to ovate or obovate, with acute base and blunt or acute summit, entire, thickish, drying brown, very minutely short-hairy above, more so beneath, where the midrib and secondaries are prominent, the latter 6 or 8 on a side, slender, strongly falcate. Cymes slenderly peduncled, mostly shorter than the leaves, the flowers numerous, densely crowded. Calyx-tube 1 mm. long, cupulate, the teeth a little longer, very unequal, triangular-ovate, acute, lightly spreading. Corolla-tube 8 mm. long, cylindrical, the lobes 3 mm. long, the appendages thickened and indurated, and almost continuous with the end of the lobe. Anthers attached at the summit of the tube, 2 mm. long, the basal lobes very slender, attenuate, about a third of the length. Style very slender, extending beyond the middle of the corolla-lobe.

Type collected by the author in copses of the pampas near Lake Rogagua, Prov. Beni, Bolivia, altitude 1000 feet, Oct. 28, 1921 (Mulford Explor. *no.* 1365), and deposited in the herbarium of the New York Botanical Garden. "A large shrub, with white flowers."

#### ANISOMERIS Presl

1. *A. SPINOSA* Presl, *Symb. Bot.* 2: 5. *pl.* 54. 1833. (*Chomelia Anisomeris* Muell.-Arg. *Flora* 58: 451. 1875.)
2. *A. Martiana* (Muell.-Arg.) n. comb. (*Chomelia Martiana* Muell.-Arg. *l.c.*) Figured under the name "*C. obtusa*



Cham. & Schlchtdl." by Wawra, Bot. Ergebn. Reise Maxim. Bras. 105. *pl.* 74. 1866.

3. *A. ribesioides* (Muell.-Arg.) n. comb. (*Makanea ribesioides* Muell.-Arg. Flora 58: 453. 1875. *Chomelia ribesioides* Benth.; Mart. Flor. Bras. 6<sup>5</sup>: 40. *pl.* 5. 1881.)
4. *A. polyantha* (Blake) n. comb. (*Chomelia polyantha* Blake, Contr. U. S. Herb. 20: 532. 1924.)
5. *A. brachyloba* (Standley) n. comb. (*Chomelia brachyloba* Standley, Contr. U. S. Nat. Herb. 18: 136. 1916.) Pittier's specimen from Vic. Valencia, Venezuela, labelled as above by Standley, is the only representative of the species seen by me. Smith's specimen, there cited, is a *Chomelia*, described above as *C. longicaudata* n. sp.
6. *A. boliviana* (Standley) n. comb. (*Chomelia boliviana* Standley (*l.c.*). *Chomelia tenuiflora* Benth. ex Rusby Mem. Torrey Club 3<sup>3</sup>: 45. 1893.)

Gleason's *no.* 872, from banks of the Essequibo River, Blackstone, British Guiana, is a species of *Anisomeris*. N. E. Browne says of it "Very near *C. angustifolia* Benth.," to which species Standley refers it. If this is identical with Bentham's species, the latter must be referred to *Anisomeris*.

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## Notes on Fabaceae—IV

PER AXEL RYDBERG

### XYLOPHACOS Rydberg

The genus was originally based on two species, *Astragalus missouriensis* and *A. Shortianus*, of which the latter was regarded as the type. Later the author (Bull. Torrey Club 32: 661-2. 1906, and 40: 48-49. 1913) extended the genus to include practically Gray's and Watson's sections ARGOPHYLLI and ERIOCARPI or Sheldon's LANOCARPUS and SERICOPHYLLUS. Dr. Gray, to whom the fruit was unknown, included erroneously *A. Arthur-Schottii* in the former; likewise Watson included *A. pubentissimus* and *A. Beckwithii*. Sheldon misplaced several species, as *A. dorycnoides*, which he had misunderstood, *A. Thompsonae*, which he renamed *A. syrticclus*, *A. triquetrus*, *A. Beckwithii*, *A. artemisiarum*, *A. mokiaceus*, *A. ursinus*, *A. gilensis*, *A. Reverchoni*, and *A. pubentissimus*. I am now inclined to exclude also *A. Parryi* from the genus.

I can not see why Gray (followed by Watson and Sheldon) placed one of his sections in the subgenus *Euastragalus* and the other in the subgenus *Phaca*. Species with the pod more or less sulcate on the lower suture are found in both sections, but none have even a partial partition. The only difference is the pubescence of the pod, and *A. glareosus* and *A. arnophyllus* connect the two groups. Jones in his latest work "Astragalus," united the two sections under ARGOPHYLLI, but erroneously included *A. desperatus* in it.

The genus is characterized by its woody or leathery pod, one-celled and somewhat inflated, without any partition, long cylindric calyx-tube longer than the teeth, comparatively narrow petals, with the claws (except that of the banner) longer than the blades. All the species are perennial with a woody caudex, usually with short stems and most of them with silvery canescent foliage. The genus is wholly North American.

Pod strigose, short-pilose, or glabrous.

Exocarp of the fruit not spongy; stem evident,  
but often short.

Pod more or less curved, or at least decidedly  
oblique.

- Leaves sparingly hairy or glabrous,  
scarcely canescent. I. IODANTHI
- Leaves densely silvery canescent on  
both sides. II. CYANEI
- Pod straight or nearly so; leaves silvery. III. MISSOURIENSES
- Exocarp of the fruit spongy at least in age; plant  
subacaulescent. IV. PYGMAEI
- Pod long-villous.
- Corolla purple or ochroleucous.
- Pubescence of the leaves strictly appressed. V. ERIOCARPI
- Pubescence of the leaves loosely villous. VI. GLAREOSI
- Corolla crimson. VII. COCCINEI

## I. IODANTHI

- Calyx more or less black-hairy; pod more or less stri-  
gose; leaves strigose or glabrous.
- Leaflets glabrous or sparingly hairy on the  
margins and veins; pod mottled. 1. *X. iodanthus*
- Leaflets strigose beneath; pod not mottled. 2. *X. cibarius*
- Pod 2.5-4 cm. long, long-acuminate. 3. *X. cuspidocarpus*
- Pod 2-2.5 cm. long, abruptly acute at each  
end. 4. *X. puniceus*
- Calyx white-hairy, pod short-pilose or glabrous. 13. *X. iodopetalus*
- Leaflets, calyx, and pod short-pilose.
- Leaflets, at least below, and calyx long-pilose;  
pod glabrous.

1. *Xylophacos iodanthus* (S. Wats.) Rydberg. (*Astragalus iodanthus* S. Wats. Bot. King Exp. 70. 1871.)

This species is distinguished from all the rest in the very scant pubescence, and in flower it simulates very closely some species of *Cysium*, as for instance *C. diphysum*. The fruit is narrow and resembles that of *Astragalus palans* Jones, but is not 2-celled. Jones (*Astragalus* 203. 1923) made the following remark: "The valves of the pod often curl out like rams' horns, hence arose my name 'arietinus.'" It seems as if Jones at the time thought that his *A. arietinus* was the same as *A. iodanthus*, though he had already before rightly referred it to *A. cibarius* Sheldon.

NEVADA: West Humboldt Mountains and Virginia City, *Watson* 269; Empire City, *Jones*, 10, 3837; Hunter Creek Canon, *Kennedy* 1600; Clover Mountains, *Heller* 9082; Miller Mountain, *Shockley* 300; Reno, *Jones*, in 1897; Virginia City, *Bloomer*, in 1863; Kingston Canyon, *Hitchcock* 909.—CALIFORNIA: Sierra Nevada Mountains, *Lemmon*, in 1875.

2. *XYLOPHACOS CIBARIUS* (Sheld.) Rydberg. The first mentioning of this species was by Watson in the Botany of the King's Expedition, where it was regarded as a form of the preceding. As a species, *Astragalus cibarius*, it was described by Sheldon who gave a specimen collected by Jones in the Utah Valley as the type. A year later Jones described it under the name *A. arivertinus*, his own specimens no. 55540 from Fairview being the type.

UTAH: Spanish Fork, and Utah Valley, *Fremont*; *Beckwith*; *Siler*; *Jones*, in 1880; Great Salt Lake, *Stransbury*; Antelope Island, *Watson* 270; Utah Valley, *Jones* 1679; Logan, *Mulford* 23, 48; Wellsville, 37; Salt Lake City, *Rydberg* 6633; *Leonard*, in 1883 and 1884; *Stokes*, in 1901; Oxford, *Leonard* 10; Logan, *C. P. Smith* 2322; *Mrs. Clemens*, in 1908; *Renselear*, in 1889; *W. W. Jones* 165; *Garrett*, in 1903; 1734.—COLORADO: Paonia, Delta County, *Osterhout* 4522.—WYOMING: Evanston, *A. Nelson* 2968.—MONTANA: Bozeman, *Blankinship*, in 1900; San Coulee, *R. S. Williams* 745; Galatin County, *Vogel* in 1901.—IDAHO: Pocatello, *Mrs. Soth* 43.

3. *XYLOPHACOS CUSPIDOCARPUS* (Sheld.) Rydberg. *Astragalus cuspidocarpus* was described from specimens collected by R. S. Williams at Grafton, Montana. It is closely related to the former and mainly distinguished by the shorter more abruptly acute pod and smaller flowers. A specimen, *Leiberg* 171, was distributed under this name, but it belongs to a species of *Cystium*. Led astray by this specimen, Jones referred *A. cuspidocarpus* first to *A. lentiginosus* Dougl. and later to *A. diphysus* Gray (*Astragalus* 125. 1923), but in the same publication, p. 213, he made it a variety of *A. Missouriensis*, confusing it with *A. Shortianus minor* A. Gray.

MONTANA: Bozeman, *Chestnut & Jones* 203; Blackfoot River, *Canby* 75; Anaconda, *Blankinship* 675.—IDAHO: Picabo, Blaine County, *Macbride & Payson* 2922.—WYOMING: Mammoth Hot Springs, *Burghlehaus*, in 1893; Yellowstone Park, *Mearns* 645, 805.

4. *XYLOPHACOS PUNICEUS* (Osterhout) Rydberg. The type of this was collected at Trinidad, Colorado. Jones (*Astragalus*, in the index) referred it to *Astragalus missouriensis*, but evidently had not seen any specimens. *X. punicens* is not closely related

to any of the other species, is characterized by its tall stems, short, spreading pubescence, which extends even to the fruit. It is placed in the present group on account of its rather thin, arcuate, mottled pod, and rather sparse and spreading, not silvery canescent pubescence. Perhaps it should have constituted a group by itself.

COLORADO: Trinidad, *Osterhout* 1737; near Fishers Peak, Trinidad, *Miss Beckwith* 101.—OKLAHOMA: Kenton, Cimarron County, *G. W. Stevens* 468.

## II. CYANEI

Pod tapering at the base, narrowly lanceolate-lunate, decidedly arcuate.

Leaves linear, obtuse; racemes elongate; calyx black-hairy.

5. *X. Casei*

Leaves oval or ovate to elliptic or lanceolate, if narrow, acute; racemes mostly short.

Pod mottled, 2-3 cm. long; calyx more or less black-hairy, the teeth less than half as long as the tube; leaflets oval, acute.

6. *X. Zionis*

Pod not mottled, 3-4 cm. long.

Calyx-teeth less than half as long as the tube; leaflets obovate or oval, obtuse or acutish; bracts 2-3 mm. long.

Leaflets oval, or elliptic, or narrowly obovate.

Calyx white-hairy; pod forming nearly half a circle.

7. *X. amphioxys*

Calyx black-hairy, pod forming one-fourth to one-third of a circle.

8. *X. melanocalyx*

Leaflets broadly obovate.

18. *X. Tidestromii*

Calyx more or less black-hairy, the teeth more than half as long as the tube; leaflets lanceolate, very acute; pod about 8 mm. wide, slightly arcuate; bracts 5-8 mm. long.

9. *X. aragalloides*

Pod rounded, obtuse, or merely acute at the base, obliquely lanceolate or ovate, less arcuate.

Corolla white or ochroleucous; calyx with mixed black hairs; leaflets mostly oblong or elliptic.

10. *X. Webberi*

Corolla usually purplish; calyx mostly white-hairy.

Leaflets elliptic to obovate; pod strictly strigose.

Calyx loosely pubescent.

Pod pubescent; leaves pubescent on both sides.

Pod 3-4 cm. long, arcuate, sulcate on the lower suture; corolla more than 2 cm. long.

11. *X. Shortianus*

Pod 2-2.5 cm. long, slightly arcuate, not sulcate; corolla less than 2 cm. long.

12. *X. pephragmenus*

Pod glabrous; leaves often glabrate above at least in age.

Calyx-lobes about half as long as the tube.

13. *X. iodopetalus*

Calyx-lobes less than one-fourth as long as the tube.

14. *X. remulcus*

Calyx with strictly appressed hairs.

Pod lance-ovoid, 2 cm. long or more.

Leaflets elliptic or elliptic-obovate.

Calyx black-hairy, peduncles 3 dm. long; plant green.

15. *X. Chloridae*

Calyx white-hairy; peduncles 1-2 dm. long.

Calyx-teeth about one-third as long as the tube.

16. *X. cyaneus*

Calyx-teeth less than one-fourth as long as the tube.

17. *X. brachylobus*

Leaflets broadly obovate....

18. *X. Tidestromii*

Pod broadly ovoid 1.5 cm. long or less.

Leaflets 9-13, obovate, about 1 cm. long; pod broader than high.

19. *X. castaneaeformis*

Leaflets 15-25, oval or elliptic, 5-7 mm. long; pod higher than broad.

20. *X. tephrodes*

Leaflets lance-oblong, acute; pod hirsutulous.

21. *X. argophyllus*

5. *Xylophacos Casei* (A. Gray) Rydberg. (*Astragalus Casei* A. Gray. Bot. Calif. 1: 154. 1876.)

This species was described from specimens collected near Pyramid Lake, Nevada, but its range extends southward to the

Death Valley, California. Dr. Gray associated it correctly with *Astragalus iodanthus* and *A. Webberi*, notwithstanding the narrow leaflets. The pod resembles that of the former but is thicker, less mottled, and pubescent. The pubescence of the leaves is that of *X. Webberi*, but the pod is more ob-compressed, narrower, and more tapering at the base. The species is perhaps more closely related to *X. amphioxys*, differing in the narrower leaflets, elongate inflorescence, and black-hairy calyx. Jones (*Astragalus* 147. 1923) placed it with *Astragalus Grayi* and *A. pectinatus*, with which it has no close relationship.

NEVADA: Pyramid Lake, *Lemmon & Case*; Candelaria, *Jones* 354; Hawthorn *Jones* 3834, *Lemmon* 67; Gold Mountain, *Purpus* 5984.—CALIFORNIA: Owens Valley, *Jones*, in 1897; Panamint Mountains, *Coville & Funston* 747; Inyo County, *Hall & Chandler* 7154; San Bernadino Mountains, *Jones* 6235.—WASHINGTON: Walla-Walla, *Brandegee* 720.

6. XYLOPHACOS ZIONIS (M. E. Jones) Rydberg. This species is evidently related to *X. amphioxys* and *X. aragalloides*, though the pod is less tapering at the base, shorter, and distinctly mottled.

UTAH: Springdale, *Jones* 5239, 5249 g and h.

7. XYLOPHACOS AMPHIOXYS (A. Gray) Rydberg. *Astragalus amphioxys* A. Gray was based on *A. Shortianus* var.? *minor* A. Gray, Proc. Am. Acad. 6: 211, "*magna pro parte*" and *A. cyaneus* S. Wats. Am. Nat. 9: 270. The latter included *Parry* 46 and 49. Dr. Gray also cited the following collectors: "Thurber, Parry, Palmer, &c." Turning to the publication of *A. Shortianus minor* we find that it was based on "*A. cyaneus* A. Gray Pl. Fendl. p. 34 (*magna pro parte*)."  
*A. cyaneus* A. Gray was wholly based on *Fendler* 148. It seems therefore that, if literally interpreted, *A. amphioxys* would be a mere substitute for *A. cyaneus* A. Gray. Evidently Dr. Gray did not mean *A. cyaneus (magna pro parte)* in *Plantae Fendlerianae*, but *A. cyaneus (magna pro parte)* as he had extended his conception in the mean time, which included *A. cyaneus* of the Botany of the Mexican Boundary Survey, i. e. *Thurber* 295 from Dona Ana, New Mexico, and *Mexican Boundary Survey* 255 from El Paso. The latter number was omitted in the published volume, but is inserted in lead-pencil in Dr. Torrey's private copy. Both of

these I regard as typical *A. amphioxys*. Thurber's specimens (in flower only) are the first mentioned under that species, and should be regarded as the type, if *A. amphioxys* is to be limited to the first synonym mentioned. Fendler 148 can not be so regarded as it does not agree with Dr. Gray's description.

The second synonym under *A. amphioxys* may be considered by some botanists, as Parry 46 and 49 are mentioned first, merely to connect with the reference in the American Naturalist. If so there will arise another serious trouble, for Parry 46 and 49 are not alike. The former is cited first and it agrees best with the description having "foliis saepius oblongis acutis." I regard this number as belonging to *X. aragalloides*; while no. 49 is the same as Thurber 295 and Mexican Boundary Survey 255, or as I take it, *X. amphioxys*. In the Gray Herbarium no. 49 has been changed by Dr. Gray to *A. amphioxys* Gray n. sp. while no. 46 remained unchanged as *A. cyaneus*.

It is therefore best to regard Thurber 295 as the type. In this case the specimens cited by Gray, viz. "Thurber, Parry, Palmer &c." belong to *X. amphioxys* except Parry 46. Sheldon has determined Parry 49 in the Columbia Herbarium as *Astragalus crescenticarpus* but it was not included in the original description and does not seem to fit it. The same number in Gray Herbarium he determined as *A. Shortianus*, and no. 46 as *A. amphioxys*.

TEXAS: El Paso, Mexican Boundary Survey 255: Vasey, in 1881.—NEW MEXICO: Rio Grande, Thurber 295, Frontera, Mexican Boundary Survey (Parry) 255; Albuquerque, Winnee Harward, in 1900; Kammerer 37.—ARIZONA: Palmer 105, 115, in 1876; Grand Cañon, Lemmon 4167; Franconia, Jones, in 1903.—UTAH: St. George, Parry 49; Washington, Jones, in 1880.—NEVADA: Meadow Valley Wash, Jones, in 1914.—CHIHUAHUA: Paso del Norte, Pringle 201.

8. *Xylophacos melanocalyx* Rydberg, sp. nov. (*Astragalus amphioxys* M. E. Jones, *Astragalus* 214, in part. 1923. *Astragalus amphioxys* × *Layneae* M. E. Jones, *Astragalus* 215. 1923.)

Perennial, with a caespitose calyx; stems many, 2-7 cm. long, decumbent or ascending, white-strigose, densely covered with leaves; leaves 5-10 cm. long, ascending or spreading; stipules deltoid, 5-8 mm. long, white-strigose; leaflets 11-19, oval or obovate, 5-10 mm. long, 2-5 mm. wide, white silky-strigose on



both sides, obtuse at each end; peduncles 7-15 cm. long, erect, white-strigose; bracts lanceolate, 2-3 mm. long, membranaceous; flowers subsessile; calyx black-hairy, the tube 6-7 mm. long, 3-3.5 mm. broad, the lobes deltoid-subulate, 2 mm. long; corolla bluish-purple, 15-18 mm. long; banner obovate, moderately arched; wings shorter, the blade oblong, acutish, with a large reflexed basal auricle; keel-petals nearly as long as the keel, the blades lunate, rounded at the apex; pod crescent-shaped, about 3 cm. long, 1 cm. broad and 5-7 mm. deep, cross-wrinkled, white-strigose with somewhat kinked hairs.

Type collected at Copper Mine [west of St. George], Utah, April 4, 1894, *Jones 5009* (Pomona College herbarium).

The type constituted a part of Jones' *Astragalus amphioxys*  $\times$  *Layneae*. The plant is evidently related to *X. amphioxys* and might have been made a variety thereof, differing mainly in the black-hairy calyx, darker colored corolla and comparatively broader and less curved pod. I think that Jones is mistaken, however, in regarding it a hybrid with *Astragalus Layneae* A. Gray, i.e. *Hamosa Layneae* (A. Gray), the plant having no feature characteristic to that species and not found in *X. amphioxys*. In fact three numbers of Jones' own collecting and named by him simply as *A. amphioxys* belong to *X. melanocalyx*. One of these was collected at the same locality and the same date as the type of the so-called hybrid. To me it seems to be a part of the same collection. *Jones 5009* from the Copper Mine was assigned as the type as it is the only one having an old fruit.

UTAH: Copper Mine, April 4, 1894, *Jones 5009* (named *H. amphioxys*  $\times$  *Layneae*); Beaver Dam Mountains, *Tidestrom 9344*.—ARIZONA: Beaverdam, April 5, 1894, *Jones 5009*. Chimehuvis, April 21 and 23, 1903, *Jones* [one sheet (Pomona College number 25956) of the former was named *A. amphioxys* the other (no. 45600) was named *A. amphioxys*  $\times$  *Layneae*]; Vicinity of Kayenta, *John Welterill*, in 1922.

9. XYLOPHACOS ARAGALLOIDES Rydberg. Jones gives this as a synonym of *Astragalus amphioxys*, which is true only in part as to *Parry 46*. See notes under the preceding species. It differs from the same in the characters given in the key. Besides the hairs of *X. aragalloides* are filiform cylindric, not tapering at both ends, or as Jones calls them "pick-shaped" in describing *A. amphioxys*.

UTAH: St. George, *Jones 1633*; *Palmer 101*, in 1877; *Parry 46*.

10. *Xylophacos Webberi* (A. Gray) Rydberg. (*Astragalus Webberi* A. Gray, Bot. Calif. 1: 154. 1876.)

This species resembles somewhat *X. cibarius* and *X. cuspidocarpus* in general appearance and in the flowers, but is more hairy, and the pod resembles more that of *X. Shortianus*.

CALIFORNIA: Plumas County, *Mrs. Ames*, in 1875; *Lemmon* 74; *Mrs. Clemens* in 1820; *Mrs. Austin*.

11. *XYLOPHACOS SHORTIANUS* (Nutt.) Rydberg. This is characterized by the broad, silvery leaflets, the large corollas, the silky-villous rather than strigose calyx, and the large pod, rounded at the base, strongly arcuate, more or less sulcate on the lower suture and obcompressed except at the tip.

WYOMING: Telephone Canon, *A. Nelson* 54; Albany County, *A. Nelson* 2808, 7021; Laramie Hills, *E. Nelson* 54, 227; Laramie Plains, *Osterhout*; Uintah County, *Stevenson* 8.—COLORADO: Boulder, *Patterson*; Clear Creek, *Hall & Harbour*; Colorado Springs, *Sturgis*, in 1915; *Jones* 80; without locality, *Hulse*, in 1870; *Fremont*; Wet Mount Valley, *Brandegee*, in 1873; Morrison, *Clokey* 3108; Boulder County, *Tweedy* 5639, 5155; Fort Collins and vicinity, *Cowen*, in 1896; *C. F. Baker*, in 1896; Ute Pass, *Biltmore Herbarium* 1492; Clear Creek, *Coulter*; Denver, *Rydberg & Vreeland* 5976; Grand Junction, *Crandall*, in 1898; Monument, *Johnston & Hedgecock* 667; Howe's Gulch, *Crandall*, 288; Colorado Springs, *Eggleston* 11164; La Porte, *Crandall* 776; Golden, *Letterman*, in 1885; Bronson, *Eggleston* 20170.—NEW MEXICO: Emory Gap, Union County, *Eggleston* 20159.

12. *Xylophacos pephragmenus* (M. E. Jones) Rydberg. (*Astragalus pephragmenus* M. E. Jones, *Zoe* 4: 267. 1893.)

The specimen in the National Herbarium, marked in Jones' own handwriting, "Type Specimen!" represents a rather stout branch with unusually large stipules, but otherwise I can not see that it is specifically distinct from the common form represented by *MacDougal* 27 and 199. It is not closely related to *A. argophyllus*, of which Jones made it a variety in his revision of *Astragalus* (p. 208).

Two years later Jones described *Astragalus intermedius* (Proc. Calif. Acad. II. 5: 656. 1895), based on specimens in flower in the National Herbarium, collected by Palmer in Arizona. On

the same sheet there is mounted an envelope containing old fruit of some species of true *Astragalus* (perhaps *A. mogollonicus* or *A. marcidus*); from these pods the description of the fruit was drawn. There is no evidence however, that these pods belonged to the same plant. Three years later Jones changed the name to *A. Phoenicis* (Contr. W. Bot. 8: 12. 1898) as the name *A. intermedius* was preoccupied. Jones has distributed two sets of specimens determined as *A. Phoenicis*. One set from Skull Valley, collected April 28, 1903, matches the type of *A. intermedius*, but has fruit like those of *MacDougal* 27 and 199. In his "Astragalus," Jones transferred these to *A. remulcus*, the original of which had glabrous pods. The other set from Chloride, Arizona, represents a much larger plant, almost green and with black-hairy calyx. This evidently afterwards became the type of *A. remulcus Chloridae* (*Astragalus* 210. 1923).

The type of *Xylophacos lenophyllus* Rydb. was mistaken for *A. remulcus* M. E. Jones and Jones included it in his description of that species in his revision of *Astragalus*. It differs, however, in the pod, which is pubescent, and in the leaflets which are pubescent on both sides. It is a smaller plant than *X. Shortianus*, has smaller and not so coriaceous pods, thin-walled and not sulcate on the lower suture, and shorter calyx-lobes. On account of the latter character it has been regarded as the same as *A. amphioxys brachylobus* A. Gray, but the latter is smaller, with a distinctly appressed pubescence, even as to the calyx.

I therefore think that *A. intermedius*, *A. Phoenicis* and *Xylophacos lenophyllus* should be regarded as synonyms of *A. pephragmenus*.

ARIZONA: Vicinity of Flagstaff, *MacDougal* 27; 199, in 1898, also in 1891; without locality, *Palmer* 102, of 1876, not of 1877. San Francisco Mountains, *Tidestrom* 961; Skull Valley, *Jones*; Flagstaff, *Rose* 12107.—NEW MEXICO: Probably near the Copper Mines [Santa Rita], *Mexican Boundary Survey* 260 (named *A. glareosus*?).—UTAH: Pindo Cañon.

13. *Xylophacos iodopetalus* (Greene) Rydberg, n. sp. (*Xylophacos stipularis* Rydb. Fl. Rocky Mts. 504, 1063, mainly. 1917. Not *Astragalus arietinus stipularis* M. E. Jones, 1895. *Astragalus iodopetalus* Greene, Ms. in herb.)

Perennial with a caespitose caudex; stems 1-2 dm. high, sparingly pilose or glabrate; leaves 1-2 dm. long; stipules large,

scarious, deltoid, 6–8 mm. long; leaflets 21–27, obovate to elliptic, 5–15 mm. long, 4–8 mm. wide, glabrate above, silky-pilose beneath; peduncles 5–10 cm. long; racemes short and dense; bracts lanceolate, 4–7 mm. long; calyx silky-pilose, the tube 8–10 mm. long, the teeth lance-subulate, 3 mm. long; corolla purple, fully 2 cm. long; banner obovate, slightly retuse; wings shorter, the blades oblong, with a large basal auricle; keel-petals still shorter, the blades broadly obliquely obovate, arched and rounded at the apex; pod lanceolate in outline, arcuate, acuminate at the apex, obtuse at the base, cross-reticulate, 2.5–3 cm. long, glabrous.

Type collected at Arboles, Colorado, June 1899, *Baker 415* (herb. N. Y. Bot. Gard.).

This resembles in some respects *X. Shortianus* and has the same loose pubescence on the calyx, but the stem is better developed, the pubescence of the leaves is looser and sparser, and the pod is glabrous. It differs from *X. remulcus* in the longer calyx-teeth, which are about half as long as the tube.

COLORADO: Sapinero, *Baker 184*; Arboles, *Baker 415*; Ceballo, *N. L. T. Nelson 23*; Montrose, *Payson 87*.—NEW MEXICO: Kingston, *Metcalf 1056*.

14. *Xylophacos remulcus* (M. E. Jones) Rydberg. (*Astragalus remulcus* M. E. Jones, Proc. Calif. Acad. II. 5: 658. 1895.)

This is closely related to the preceding. It was described from *Rusby 576*. In this the pod is young, evidently glabrous from the beginning, shorter than in the two preceding, with a very prominent upper suture, and the leaflets are glabrous above, silky-villous rather than strigose beneath. Jones' description in his "Astragalus" fits better *X. pephragmenus*, which was also included. Sheldon included it in *A. amphioxys brachylobus* A. Gray. This may explain why Jones cited the latter as a synonym. The original var. *brachylobus* is, however, evidently not the same. In general habit *X. remulcus* resembles closely *A. mokiensis* A. Gray, but the calyx is longer, the racemes shorter, and the structure of the pod different.

ARIZONA: Bangharte Ranch, *Rusby 576*; Fort Verde, *Mearns 345*; Santa Catalina Mountains, *Griffiths 2287*; Atargue de Gracia, *Wootton*, in 1906; Jerome Junction, *Marsh*, in 1905.

15. *Xylophacos Chloridae* (M. E. Jones) Rydberg. (*Astragalus remulcus Chloridae* M. E. Jones, *Astragalus 210*, 1923.)

Related to the preceeding but a larger and greener plant, with peduncles often 3 dm. long and black-hairy calyx. The type came from Chlorida, Arizona. Another specimen from Arizona, viz. *Lemmon* 3354 may belong here.

16. *Xylophacos cyaneus* (A. Gray) Rydberg. *Astragalus cyaneus* A. Gray, Mem. Am. Acad. II. 4: 34. 1849.)

This was described from flowering specimens, together with some old loose pods. The former resembles a small plant of *X. missouriensis*, but the pods resemble those of *X. Shortianus* though smaller. Gray therefore reduced the species later to *A. Shortianus minor*, though he confused with it specimens of *X. amphioxys*. Wootton & Standley regarded it as a synonym of *A. Shortianus*. Jones for some time regarded it as a synonym of *A. missouriensis* and lately (*Astragalus* 213. 1923) he made it a synonym of *A. missouriensis cuspidocarpus*, wholly misunderstanding *A. cuspidocarpus* Sheldon, which is related neither to *A. missouriensis* nor to *A. cyaneus* but to *A. cibarius*. I myself have added to the confusion by misunderstanding both *A. cyaneus* and *A. unitensis*. What I have described in my Flora of the Rocky Mountains under the name *Xylophacos unitensis* Rydb. is mostly *X. cyaneus*.

NEW MEXICO: Santa Fe, *Fendler* 148; *Heller* 3519; *Bro. Bertaud* 114; Las Vegas, *Bro. Anect* 103; Gila Forest, *Eggleston* 17001, 16955; Shiprock, *Standley* 7181; Kingman, *Vasey*, in 1881.—COLORADO: Mancos, *Baker, Earle & Tracy* 56; Wootton, *Rusby*, in 1909; Pueblo, *Rydberg & Vreeland* 5975; Grand Junction, *Crandall*; Cripple Creek, *Tweedy* 255; Albuquerque, *Mary Cooper*, in 1909; Delta, *Tidestrom* 2178.—OKLAHOMA: Woods County, *G. W. Stevens* 220; Harper County, 303, 527, 263; Beaver County, 337, 359; Cimarron County, 472; Texas County, 388.—TEXAS: Grady, Fisher County, *Shepherd*, in 1901.—ARIZONA: *Rothrock* 1112.

17. *Xylophacos brachylobus* (A. Gray) Rydberg. (*Astragalus Shortianus brachylobus* A. Gray, Proc. Am. Acad. 13: 367. 1878.)

This species was first collected by Edward Palmer (no. 115 in 1876, and no. 102, 1877) in Northern Arizona. On the latter, Dr. Gray based the variety. Jones has applied this name as a synonym of *A. remulcus*, but evidently he was in error, though

*A. remulcus* and *X. lenophyllus* both have short calyx-teeth and therefore would agree with Gray's short description. *Palmer 102*, the only specimens Dr. Gray had before him at the time, evidently must be regarded as the type.

ARIZONA: without locality, *Palmer 115*, in 1876; *Palmer 102*, in 1877; also 316; Holbrook, *Miss Zuck*, in 1896; Clifton, *Rusby*; Pinal Mountains, *Jones*, in 1890; El Tovar, Grand Cañon, *Setchell*, in 1907; Peach Spring, *Lemmon*, in 1884; Carrisa Mountains, *Standley 7477*; Winslow, *Ward*, in 1901; Petrified Forest, *Ward* in 1901; Holbrook, *Zuck*, in 1896.—NEW MEXICO: Albuquerque, *Herrick*, in 1894; Mangus Springs, *Rusby 90½*; Santa Fe, *Earle 82*; *Fendler 149*, *Edwards*; without locality, *Miss Harvard*, in 1900; Silver City, *Eggleston 19953*, *19955*.—COLORADO: Los Pinos, *Baker 426*.—UTAH: Kanab, *Mrs. Thompson*; Belknap, *Stokes* in 1900.—NEVADA: St. Thomas, *Tidestrom 8673*.

18. *Xylophacos Tidestromii* Rydberg, sp. nov. Perennial, with a deep woody root and short caespitose caudex; subcaulescent; stems 1–5 cm. long, white-woolly; leaves 5–8 cm. long, spreading, stipules broadly deltoid about 5 mm. long; leaflets 11–15, broadly obovate, 6–12 mm. long and nearly as broad, densely white, silky-villous on both sides, cuneate at the base, rounded at the apex; peduncles 5–7 cm. long; racemes 2–4 cm. long; bracts lanceolate, 2–4 mm. long; calyx with mixed white and black hairs, the tube 6–8 mm. long, the teeth subulate, 2 mm. long; corolla unknown, except the keel-petals which are 12 mm. long, the blade broadly lunate, with a large auricle, purple-tipped, and shorter than the claw; pod tapering at each end, strongly arched above the middle, strigose-canescens, cross-reticulate, about 4 cm. long, 4 mm. high and nearly 1 cm. broad.

Type collected in Charleston Mountains, Nevada, May 27, 1919, *Ivar Tidestrom 9661* (U. S. Nat. Herb. 1117336.)

This species is related to *X. amphioxys* but differs in the broader leaflets, the broader and less attenuate pod. To it is also referred the following specimen, *Goodding 2283* from Las Vegas, Nevada, which has more silky pubescence and a shorter less tapering pod, 3 cm. long.

19. *Xylophacos castaneaeformis* (S. Wats.) Rydberg. (*Asragalus castaneaeformis* S. Wats. Proc. Am. Acad. 20: 361. 1885.)

This species differs from the rest of the group in the short obliquely ovoid pod and rather few leaflets.

ARIZONA: Flagstaff, *MacDougal* 36; 66; Bill Williams Fork, *Bigelow*, on Whipple's Expedition, 1854; Williams, *Lemmon* 3262; Grand Cañon, *Toumey*.

20. *Xylophacos tephrodes* (A Gray) Rydberg. (*Astragalus tephrodes* A. Gray, Pl. Wright, 2: 45. 1853.)

This species is imperfectly known from a single specimen collected in the Organ Mountains, New Mexico by C. Wright.

21. *XYLOPHACOS ARGOPHYLLUS* (Nutt.) Rydberg. This is probably most closely related to *X. cyaneus*, but differs in the narrower, acute leaflets, the longer calyx-lobes and stipules, and the longer and coarser pubescence of the pod. It approaches *X. glareosus* and has been mistaken for it, but the pod is not villous, though the hairs are long; they are straight or nearly so.

MONTANA: Dillon, *Shear* 3438.—WYOMING: *Nuttall*; *Porter*, in 1873.—NEVADA: Ruby Valley, *Watson* 281, in part; Palisade, *Jones*, in 1882; Lewiston, *Zundle*, in 1900.—UTAH: Logan, *Garrett*, *F.* 2297, Weber Cañon, *Armstrong*, in 1912; Wasatch County, *Carleton & Garrett* 6699; Parley's Cañon, *Garrett* 2132; Juab, *Goodding* 1090; Silver Reef, *Jones* 5163 h; Monticello, *Rydberg & Garrett* 9153; Juab, *Jones* 6336 B; Logan Cañon, *C. P. Smith* 2162; Salina Cañon, *Jones* 5428; without locality, *Parry* 25; Parley's Park, *Watson* 281; Park City, *Jones*; Deep Creek, *Jones*.

*Astragalus argophyllus cnicensis* M. E. Jones is nearly typical *X. argophyllus*. *A. argophyllus Martini* M. E. Jones is a depauperate form with very short peduncles and rather broad leaflets. It is represented by the following three specimens.

IDAHO: Blaine County, *MacBride & Payson*; Soda Springs, *Martin*; Arco, *Palmer* 164.

## Germination of the spores of *Riccardia pinguis* and of *Pellia Fabbroniana*

A. M. SHOWALTER

(WITH TWO TEXT FIGURES AND PLATE 5)

The following study with the spores of *Riccardia pinguis* (L.) S. F. Gray (= *Aneura pinguis* Dumort.) was undertaken to determine the origin of the apical cell. The spores were sown on thin agar plates (about 1.3% in tap water) in shallow petri dishes, and the covers were fastened in place with strips of gummed paper. The petri dish could then be placed on the stage of the microscope and the sporelings examined without removing the cover. By the use of indices on the cover it was easy to find again a given sporeling and thus to make camera lucida sketches showing successive stages in its development.

This of course permitted the use only of the low power objective (Leitz no. 2) and the image lacked clearness. Intracellular details could not be determined and it is probable that cell divisions were apparent only after the formation of a cell wall.

The spores were sown March 23, 1923 and the cultures were kept in the Bryophyte greenhouse of the National Botanical Garden at Brussels. The temperature and light intensity were both rather low and in most cases the first division of the spores was apparent only about a month after the sowing.

The changes in the spore preceding the first division have been described by Miss Clapp (1912) and need not be repeated here. As observed in other cultures and as reported by Miss Clapp the first division of the spore is very unequal. The smaller cell then grows and divides, again more or less unequally, in a plane which intersects the previous division wall (FIG. 1,  $a_1$ ,  $b_2$ ,  $c_1$ ,  $d_1$ ), (Miss Clapp's fig. 59). The smaller of these two cells grows more rapidly than its sister and divides, again unequally, in a plane which intersects the previous wall and marks out a well defined apical cell (FIG. 1,  $a_2$ ,  $b_4$ ,  $c_2$ ,  $d_2$ ). This apical cell continues to grow and give off, alternately right and left, segments each of which is larger than the remaining apical cell, as is characteristic of the apical cell in the older plant (FIG. 1,  $a$ ,  $b$ ,  $c$ ,  $d$ ).



All these divisions beginning with the first division in the spore are unequal and in each case the smaller cell grows more rapidly and divides before its sister. The segments are given off alternately right and left except the first which is posterior to the direction of growth. This suggests that the spore itself in effect functions as an apical cell, but I have no evidence to show that its polarity is fixed, as seems to be the case in *Pellia Fabbromiana* described below.

The segments given off by the apical cell may, very early, undergo further division (FIG. 1,  $d_5$ ,  $d_6$ ) but in this experiment

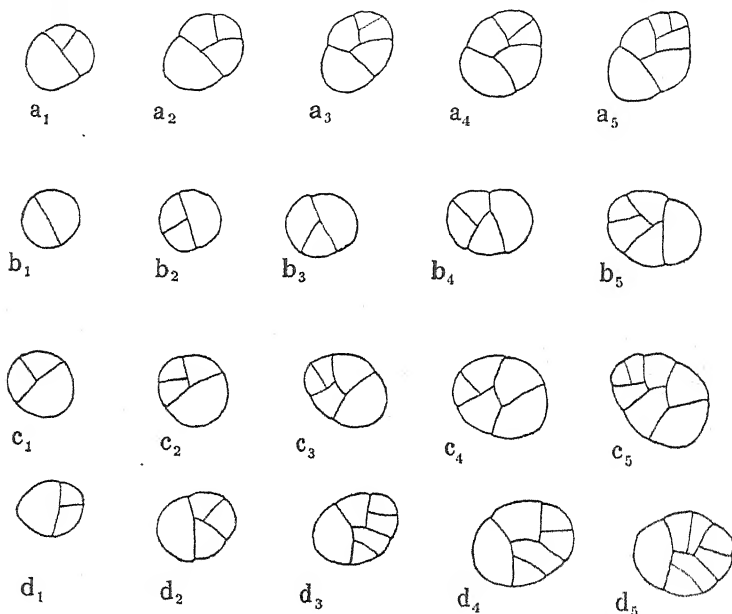


FIG. 1. Four sporelings of *Riccardia pinguis* sketched in successive stages of development;  $a_1$ ,  $b_1$ ,  $c_1$ ,  $d_1$  sketched May 5, 1923;  $b_2$ ,  $c_2$  sketched again May 7;  $a_2$ ,  $b_3$ ,  $c_3$ ,  $d_2$  sketched again May 10;  $a_3$ ,  $d_3$  May 12;  $a_4$ ,  $b_4$ ,  $c_4$ ,  $d_4$  May 17; and  $a_5$ ,  $b_5$ ,  $c_5$ ,  $d_5$ , May 19.

no case was observed in which the first segment (the posterior cell formed by the first division) had divided. An experiment described below shows however that this cell may divide.

The spores of this species may also be germinated on the slide and some of the protoplasmic changes accompanying nuclear and cell division may be observed *in vivo*. A clean slide

is sterilized in the flame of a bunsen burner or alcohol lamp and when sufficiently cooled a few drops of warm agar solution (about 1.5% in tap water) are poured on the slide. As soon as the solution begins to congeal at its edge a few freshly shed spores are dropped on the liquid surface and a clean sterilized cover slip is added. The preparation is placed in a moist chamber (petri

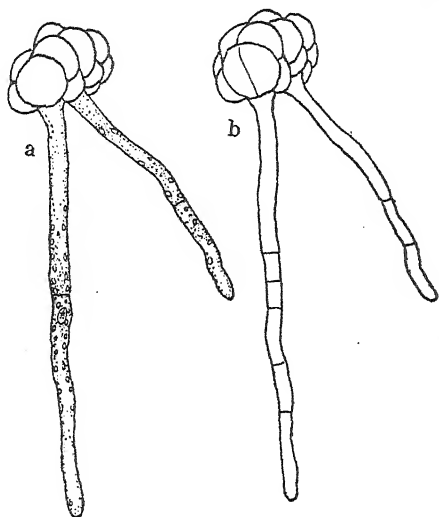


FIG. 2. Sporeling of *R. pinguis* (a) sketched May 25, and (b) again June 9. Further explanation in text.

dishes were used) before a north window. Spores in such culture-preparations underwent the first division in from ten to fifteen days. The daily variations in the temperature of the laboratory caused the agar to dry out but some of the sporelings developed to the three-celled stage.

At the time these culture-preparations were made there was on my table a watch glass with spores which had germinated in tap water and had developed to the two-celled stage—the stage at which sporelings in water culture usually die. A few culture-preparations similar to those just described were made, using these two-celled sporelings instead of freshly shed spores. In one of these culture-preparations the sporelings developed to about a dozen cells each and produced rhizoids of considerable length (FIG. 2).

The rhizoids were formed as abrupt outgrowths from cells near the posterior end of the sporeling but in no case did I find a rhizoid arising from the end cell—*i. e.* the first segment given off by the germinating spore. This cell is easily distinguished by its brownish color due to the presence of a large part of the exine of the spore which adheres to and covers all its free surface. (Miss Clapp's *figs. 61, 62*).

Disintegration of these sporelings was first noticeable in the young cells of the apical end. At about the same time that disorganization was first noticeable in the apical end, nuclear and cell divisions were observed to occur in the rhizoids and in the oldest cell—the initial segment given off by the germinating spore. FIG. 2 shows the same sporeling sketched May 25 and again June 9. At the former date the initial segment was still undivided and each of the two rhizoids had divided into two cells. At the latter date the initial segment had divided once and the larger rhizoid had divided into six cells. Other sporelings in the same culture-preparation showed rhizoids divided into varying numbers of cells. The maximum number of cells into which any one rhizoid had divided was seven. These divisions were not accompanied by growth, and in none of the rhizoids, sketched before and after the divisions had occurred, could any increase in size be detected.

Goebel (1906) describes multicellular rhizoids in *Gottschea*, which, I think, is the only other record of such rhizoids in the Hepaticae. The divisions here reported in the rhizoids of *Riccardia* have occurred, it is true, under highly special physico-chemical conditions, but these conditions probably do not exceed the range of conditions in nature.

#### PELLIA FABBRONIANA

It has long been known that the spores of *Pellia* germinate before being shed from the sporogone (Hofmeister '51, Müller '66, Leitgeb '77). Upon examining sporogones of *P. epiphylla* collected January 18, 1924, in the Forêt de Soigne near Brussels I was surprised to find the "spores" already consisting of four to eight cells each, although the sporogones were still quite small. It occurred to me to examine *Pellia Fabbroniana* Raddi, of which there were about two dozen sporogones in one of my greenhouse cultures. Since the number of sporogones available

was so small they were used only sparingly in order to get the maximum of information from the material available.

Two of these sporogones were examined the same day (January 18). One of them showed the large four-lobed spore mother cells in some of which the cell division was not yet complete (FIG. 3). The lobes of the spore mother cell (and the spores formed from them) are long ovoid with the long axis about twice as great as the median transverse diameter (FIG. 3, 4, 5). In many of these spore mother cells the spindle of the last division was still distinguishable and appeared to be composed of granular strands. The protoplasm in the immediate vicinity of the spindle was free of chloroplasts but contained numerous small refractive bodies (whether globules of liquid or more solid bodies was not determined). Chloroplasts were so numerous in the rest of the space within the cell as to obscure all other structures from view.

When these spore mother cells were placed in water one or more of the lobes of each cell burst at its distal end and allowed the protoplasm to flow out. In some cases the fissure in the cell wall was small and the outflow of protoplasm was very slow. In such cases the granules in the strands of the spindle could be seen to migrate toward the lobe from which the protoplasm was exuding. As the movement was accentuated, single chloroplasts were seen to pass along one of the strands of the spindle and to migrate over to the discharging lobe, the spindle remaining in its original form and position until a considerable quantity of the protoplasm had been exuded. This suggests that these cells might be favorable objects for microdissection studies of the structure of the achromatic spindle.

The other sporogone examined at the same time showed about half of the spores once divided, about one-fourth with an incomplete cell plate, and about one-fourth in which no indication of the division was apparent. These were mounted in water and when examined under the microscope the spores had separated from their tetrad sibs and no exospore wall was visible on them. (It was later observed that "spores" up to the time of the second division are held together in tetrads by the exospore but when placed in water this exospore ruptures at the free end of each lobe and the "spores" pop out leaving behind the four-lobed gelatinous cell wall of the spore mother cell with its echinate surface.)

The first division wall in the spore is almost longitudinal (FIGS. 4, 5). (See also Leitgeb's *fig. 10, pl. 3.*) During the later stages of this division and in the newly formed daughter cells the chloroplasts form two opaque masses (enclosing the nuclei) on opposite sides of the median part of the cell plate. In the end portions of the cells are many small refractive colorless bodies which exhibit a vigorous Brownian movement and to which is imparted a dark color when the "spore" is thrown into a fixing solution containing osmic acid.

A few sporogones from the same culture were fixed the same day, imbedded in paraffin and sectioned in the usual way. These showed, in different sporogones, spore mother cells in which the nucleus had not yet divided, one-celled spores, and two-celled "spores." Some of the one-celled spores show various stages of the first nuclear division but none were found to show satisfactorily the formation of the cell plate. The achromatic spindle of this mitosis is long and slender with its long axis coincident with the long axis of the spore. It would be interesting to know the changes which intervene between this nuclear division and the formation of the cell plate which divides the spore into two cells.

The second division occurs simultaneously in the two sister cells and divides each of them transversely (FIG. 6). Stained sections show that the achromatic spindle is longitudinal and is followed by a cell plate transecting its longitudinal axis as is usually the case in plant cells. Three of the cells resulting from the second division are about equal in size and are filled with chloroplasts, but the fourth is smaller and contains only a few chloroplasts (FIGS. 6-9). This latter cell is closely analogous in form and function to the "basal cell" in the "spore" of *Pellia epiphylla* described by Hofmeister ('51) and its position with reference to the other "spores" of the tetrad and with reference to the direction of growth shows further the appropriateness of this name.

Soon after the beginning of the four-celled condition of the "spore" the tetrads may be obtained by gently opening the sporogone in water. These tetrads show clearly that the basal cell of each "spore" is in contact with that of each of the other three of the tetrad (FIG. 7). This is evident also in stained sections of sporogones at all stages of development after the

early prophases of the second division of the "spore." The area of the "spore's" surface held in contact with its tetrads is at or near the end, but oblique to the long axis of the "spore". (FIG. 7).

The basal cell undergoes no further division although it enlarges considerably. The third division occurs almost simultaneously in the other three cells (FIG. 10). The stained preparations show in some cases a slight advance of the mitosis in the terminal cell over the mitoses in the two median cells. This division in the two median cells is always transverse, parallel to the plane of the preceding division. The terminal cell divides sometimes parallel to and sometimes at right angles to the plane of the preceding division (FIG. 10). (FIGS. 9 and 10 represent "spores" from the same sporogone examined February 9.)

The "spore" remains subcylindrical in shape and the first three divisions are all visible from one side of the "spore" (FIG. 10). In sporogones whose setae had begun the rapid elongation which normally precedes the discharge of the "spores" the latter consisted of about a dozen cells each. I am unable to say with certainty whether or not all of the six cells formed by the third division had divided, but in some cases, at least five of them had done so. In the cells of the median portion of the "spore" this division is at right angles to all the preceding divisions (FIG. 13) but in the terminal cell the dividing septum intersects only the last previous septum and the free outer surface of the cell (FIGS. 11, 12) as is typical of the divisions of the apical cell in the older plant. When such a "spore" is viewed in the plane of the earlier divisions these walls are distinguishable by their relative optical thickness (FIGS. 11, 12). In these figures the line 1.....1 represents the first division wall, 2.....2 the second, 3.....3 the third, and 4.....4 the fourth in the terminal cell, the fourth division in the cells of the median portion of the "spore" being in the plane at right angles to these and visible only when the "spore" is rotated on its long axis through 90° (FIG. 13).

Beginning in the four-celled condition of the "spore" the exospore adheres to the "spore" and is noticeable on the living "spore" chiefly by the echinate thickenings on the surface. The exospore covers the entire surface of the "spore" except that portion of the basal cell which remains in contact with the

other "spores" (FIGS. 7-10). This exospore expands as the "spore" enlarges and its presence becomes more and more difficult to detect, especially on the surface of the terminal region, as in *Riccardia* (Clapp's *figs.* 61, 62).

When "spores" of the condition represented by FIGS. 11-13 are placed in water culture the basal cell soon gives rise to a rhizoid. FIG. 14 represents such a spore after twenty-five hours in water culture; FIG. 15 represents another spore from the same culture after fifty-four hours in water. The nucleus, chloroplasts and most of the granular cytoplasm of the basal cell pass into the rhizoid.

Unfortunately the paucity of material of this species and the pressure of other duties did not permit me to follow the later stages of germination or to determine whether the cell designated *a* in FIGS. 11 and 12 continues to function as the apical cell or whether another cell may take that rôle. Leitgeb ('77) describes (his *fig.* 14, *pl.* 3) the apical cell as arising in this portion of the "spore," but Müller ('66) says that rhizoids appear at the two ends of the "spore" and that the apical cell arises in the median portion (his *figs.* 55-59, *pl.* 38). It seems probable that a high degree of plasticity exists in these cells and that any one of them (excepting the basal cell) may be capable of functioning as an apical cell if the metabolic gradient be favorably altered by external conditions.

If, as seems probable from these observations and from Leitgeb's description of the later stages of germination, the cell designated *a* in FIGS. 11 and 12 continues under normal conditions to function as an apical cell, we can hardly escape the conclusion that the spore itself is in effect an apical cell with its polarity fixed at the time of its formation from the spore mother cell. The examination of a large number of "spores," both fresh and in stained paraffin sections, shows that the plane of the first division has a definite and constant relation to the point of attachment of the spore to its tetrad sibs, and therefore to the plane of the division of the spore mother cell by which the spore is formed (FIGS. 7-10). The succeeding divisions (2....2, 3....3, and 4....4, FIG. 11) follow the order characteristic of the apical cell of the *Anacrogynae*. There is one point, rather insignificant it seems to me, which may constitute an objection to this hypothesis. The second and third segments

are in some cases given off from the same side of the apical cell (FIG. 12).

It is not possible to say from my observations what part of the apparent polarity of the spore is conditioned by factors external to the protoplasm and what part to internal factors. Here again further study may yield interesting results.

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## Explanation of plate 5

All figures were drawn with the aid of the camera lucida from living material mounted in water; at a magnification of about 630 diameters, except the last (FIG. 15) which was drawn at about 490 diameters; reduced in reproduction about  $2/5$ .

FIG. 3. Spore mother cell from sporogone grown in greenhouse, examined and drawn Jan. 18, 1924. Achromatic spindle and adjacent parts of cell and the outline of the entire cell copied as accurately as possible. Chloroplasts in terminal part of lobe at the left filled in diagrammatically.

FIG. 4. Spore from sporogone grown in greenhouse, examined and drawn Jan. 18, 1924. The first division is in progress, as nearly an optical section as could be obtained with the camera lucida.

FIG. 5. "Spore" once divided, from same sporogone as that represented in FIG. 4 and similarly drawn.

FIG. 6. Living "spore" from sporogone grown in greenhouse, examined and drawn Jan. 28, 1924.

FIG. 7. Living "spore" still attached to its tetrad sib, from sporogone collected in Forêt de Soigne, examined and drawn Feb. 12, 1924.

FIG. 8. Living "spore" from greenhouse culture, examined and drawn Feb. 2, 1924.

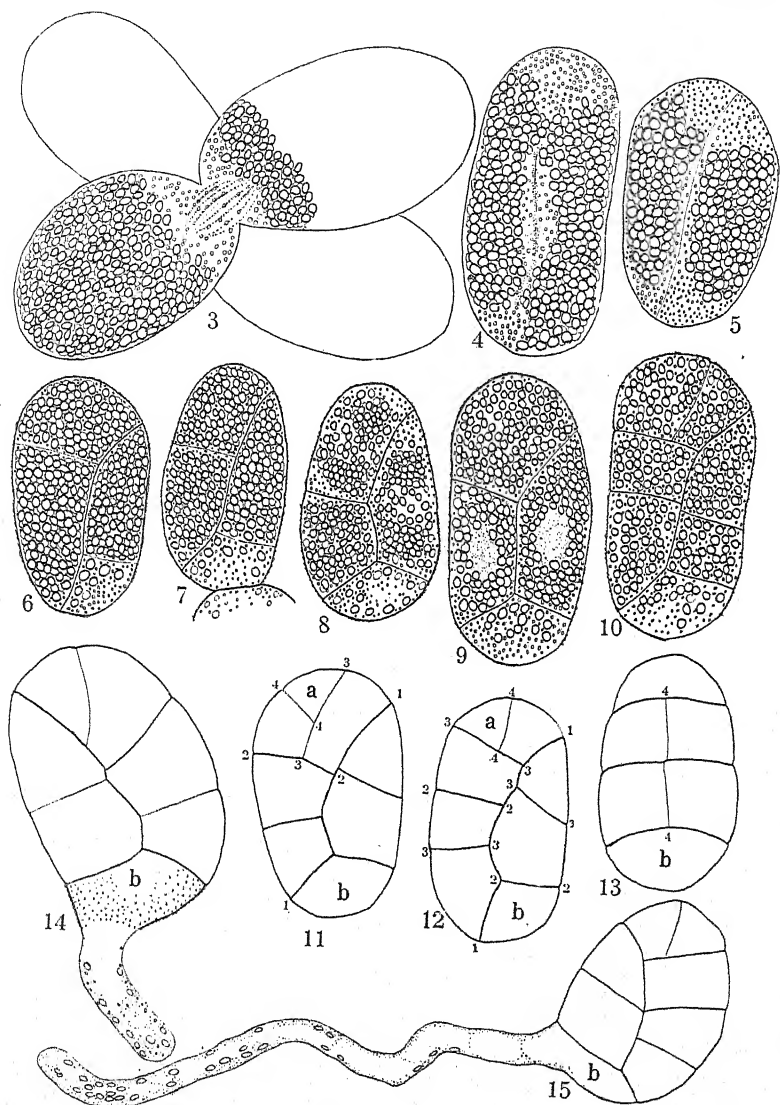
FIGS. 9, 10. Living "spores" from same sporogone grown in greenhouse, examined and drawn Feb. 9, 1924.

FIGS. 11, 12. Outlines of living "spores" from same sporogone grown in greenhouse culture, examined and drawn Feb. 26, 1924, just before the time of dissemination. The line 1...1 represents the plane of the first division; 2...2 that of the second; 3...3 that of the third; and 4...4 that of the fourth division in the terminal cell. The basal cell *b* formed by the second division has undergone no further division.

FIG. 13. Outline of living "spore" from same sporogone as those in FIGS. 11 and 12, "spore" rotated  $90^\circ$  showing fourth division in cells of median portion.

FIG. 14. Living "spore" after twenty-five hours in water culture. The basal cell (*b*) has begun to elongate to form a rhizoid.

FIG. 15. Living "spore" after fifty-four hours in water culture.



PELLIA FABBRONIANA



# Anomalies in maize and its relatives---III

## Carpellody in maize

PAUL WEATHERWAX

(WITH TEN TEXT-FIGURES)

Two strains of corn, received in the spring of 1923 from P. C. Mangelsdorf, have a type of "defective" grain whose morphology has apparently not yet been described. The anomaly

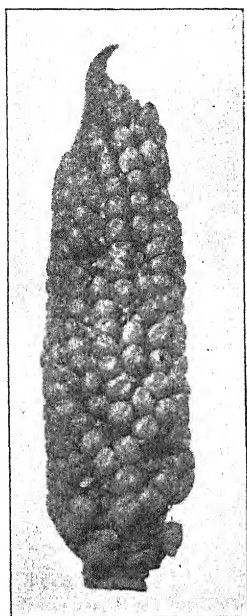


FIG. 1. An ear of maize with "defective" grains,  $\times \frac{1}{2}$ .

originated independently in two inbred lines of ordinary field corn, and is inherited as a recessive plant character. Two generations of plants have been grown from these seeds, and all evidences indicate that the peculiarity is due to the metamorphosis of rudimentary stamens of the female flower into imperfectly formed pistils.\*

The resulting structure has the appearance of a very slender grain of the "shoe-peg" type (FIGS. 1 and 2). At maturity it resembles the empty shell of a small normal grain; but examination during development shows merely a lateral sinus, and no true ovarian cavity formed by infolding or invagination (OS, FIGS. 4-6 and 10). The enclosed cavity (SC, FIG. 10) is formed by the breaking down of the parenchyma of the interior late in development. The ovary-like portion is surmounted by a style, often as much as 8 or 10 cm. long. The distal portion of this style is stigmatic and often simple in structure, having but a single vascular strand and ending in a single tip. Its basal portion, however, is usually duplex in structure, like a normal "silk" (FIGS. 8, 9). Whether or not this indicates a homology between this organ and the

\* This occurrence is commonly known as *pistillody*, but *carpellody* seems to be a better designation, at least in this instance. See Worsdell, W. C. Principles of plant teratology 2: 182-186. London, 1916.

normal style is not evident at present. This style is often accompanied by one or more, shorter, filiform appendages without vascular bundles or stigma hairs (*L* and *LL*, FIGS. 7 and 8).

In most of the cases examined only one of the lateral rudimentary stamens was metamorphosed (FIGS. 4, 5); but in a very considerable number both were affected (FIG. 2), and in a few

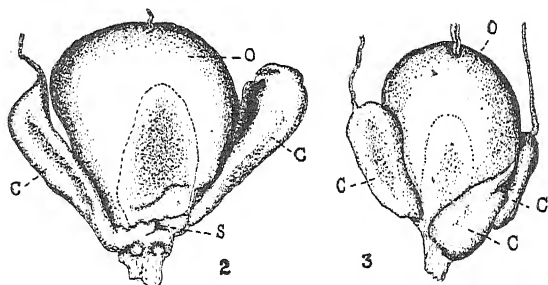


FIG. 2. Mature normal grain with two "defective" grains,  $\times 5$ .

FIG. 3. Flower with three carpellodia, near the time of fecundation,  $\times 12$ . *O*, ovary; *CC*, carpellodia; *S*, dorsal rudimentary stamen.

flowers the dorsal member also (FIG. 3). In no case observed was the dorsal stamen alone metamorphosed. Spikelets showing all these degrees of metamorphosis of the rudimentary androecium were commonly associated on the same ear with numerous spikelets having normal pistillate flowers (FIG. 1).

These transformed structures seem to be stimulated to full development by fecundation in the ovary at whose base they are attached. None have been found except in the upper (functional) flower of the spikelet. They approximate normal grains in length only when fecundation has occurred and a normal seed has developed in the ovary of the same flower. This indicates that pollination has an essential but indirect effect in the development of the anomaly.

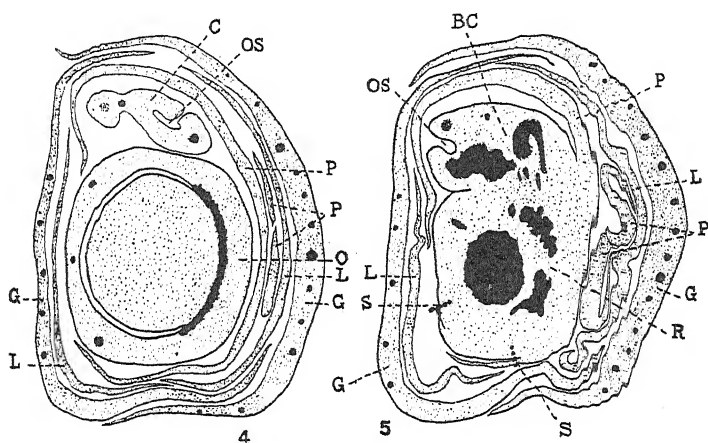
No attempt has been made to pollinize the "silks" of these supernumerary carpels; and, because of their structural limitations, it was obviously not necessary to subject the fully developed "defective" grains to germination experiments.

A case similar to this, but in the wheat plant, has been reported by Leighty and Sando.\* Here the character is ap-

\* Leighty, C. E. and Sando, W. J. Pistillody in wheat flowers. *Jour. Hered.* 15: 263-268. f. 15, 16. 1924.

parently not hereditary. Otherwise the two characters are much alike, in so far as they have been examined, even to the duplicate nature of the style in some cases, and the indirect influence of fecundation.

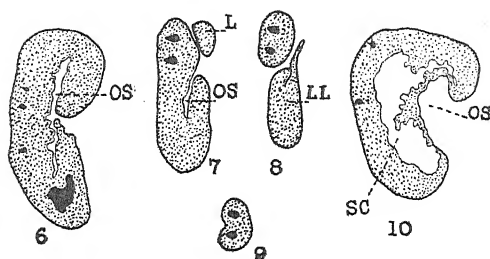
In the light of Miss Walker's theory\* as to the constitution of the gynoeceum of some grasses, the failure of these modified organs to develop into functional pistils might be attributed to



FIGS. 4 and 5. Transverse sections of a pistillate spikelet, having one carpellodium,  $\times 15$ . FIG. 4 is through the upper part of the ovary; FIG. 5 is through the receptacle of the flower. GG, glumes; LL, lemmas; PP, paleas, that of the lower (aborted) flower being two-lobed; O, ovary of the functional pistil; C, carpellodium; BC, base of carpellodium at place of attachment to receptacle; OS, ovarian sinus; R, receptacle of flower; SS, positions of the two unchanged rudimentary stamens. The vascular tissue is shown in black.

the fact that they consist of single carpels, while the true pistil is tricarpellary. But this would not explain the carpellodia in maize having duplex styles, or those in wheat having two styles. It was thought that in maize the duplex carpellodia that occur might be the result of the fusion of pairs of organs in development; but in every such case examined, the other two stamens could be accounted for (SS, FIG. 5). Therefore, unless the

\* Walker, Elda R. On the structure of the pistils of some grasses. Univ. Nebraska Studies 6: 203-218. pl. 1-5. 1906.



FIGS. 6-9. Transverse sections through a carpellodium at different levels,  $\times 15$ . FIGS. 6 and 7, the lowest sections, show the ovarian sinus, *OS*; FIGS. 7 and 8 show the formation of two lobes, *L* and *LL*, the former disappearing below the level of FIG. 8, and the latter below the level of FIG. 9. The section of the stylar portion (FIG. 9) is almost indistinguishable from that of a normal style. FIG. 10. Transverse section of a matured "defective" grain,  $\times 15$ . The cavity in this structure, *SC*, is schizogenous in the parenchyma; the ovarian sinus, *OS*, corresponds to the true ovarian cavity.

double vascular systems and other duplex characteristics of these carpellodia be regarded as false suggestions of homology, a serious inconsistency is yet to be eliminated.

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# INDEX TO AMERICAN BOTANICAL LITERATURE

1920-1925

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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BULLETIN  
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MAY 1925

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Studies on the flora of northern South America—V\*

H. A. GLEASON

MISCELLANEOUS NEW OR NOTEWORTHY SPECIES

The herbarium of the New York Botanical Garden contains thirteen species of *Dioscorea* from British Guiana and about as many more have been reported in literature. Among our thirteen are three undescribed species and one which requires a new name.

*Dioscorea lanosa* n. sp. Stem herbaceous, twining to the left, sparsely and finely villous near the nodes; petioles channeled above, thinly villous, 25–30 mm. long; leaf-blades elliptic from a cordate base, the largest 95 mm. long and 57 mm. wide, excluding the basal lobes, which are 7–8 mm. long, broadest near the middle, abruptly acuminate into a short point, glabrous above, thinly villous beneath, especially along the primary and secondary veins, 7-nerved, the first, second, and third confluent at the apex, the fourth and fifth arcuately spreading and extending to or beyond the middle of the leaf, the sixth and seventh barely surpassing the basal lobes, bifid or usually trifid near the base; pistillate spikes not seen; staminate spikes single or paired in the axils, unbranched, 10–17 cm. long, the rhachis strongly angled, thinly but conspicuously villous; flowers in clusters of two to five; pedicels 2–4 mm. long, angled, recurved-spreading, densely villous, each subtended by an ovate-triangular long-acuminate bract, which is pubescent on the back and thinly wing-margined; perianth campanulate, about 1.5 mm. long, weakly angled or nearly terete, the lobes united for two fifths of their length, oblong-ovate, acute, densely villous without, glabrous within; stamens 6, inserted at the base of the perianth-tube and about equaling it in length; filaments erect and connivent at base, abruptly spreading near the slightly enlarged apex; style-rudiment apparently none.

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\* Contributions from the New York Botanical Garden, no. 271.  
[The BULLETIN for April (52: 119–180) was issued 18 May 1925.]

Type, *La Cruz* 3875, collected along the Wanama River, Northwest District, lat.  $7^{\circ} 45' N.$ , long.  $60^{\circ} 15' W.$ , and deposited in the herbarium of the New York Botanical Garden.

*Dioscorea lanosa* is closely related to *D. pilosiuscula* Bertero, and is distinguished from it by the prominent basal sinus of the leaf, the fourth and fifth veins arcuately spreading, the acute lobes of the perianth, and the villous rhachis.

*Dioscorea oblonga* n. sp. Stem herbaceous, angled, glabrous, twining to the right; petioles about 5 cm. long, minutely verrucose; leaf-blades broadly cordate-triangular with a deep basal sinus, the largest 10 cm. wide, sharply acuminate, glabrous, the basal lobes broadly rounded with a broad obtuse sinus, first, second, and third veins extending to the apex, fourth and fifth arcuately spreading and reaching past the middle of the leaf, sixth and seventh conspicuously bifid and not extending beyond the basal lobes; staminate spikes in a loose panicle, paired or occasionally single, slender, unbranched, 9–12 cm. long; bracteal leaves ovate-lanceolate, truncate at base, long-acuminate, 10–25 mm. long, 2–12 mm. wide, on petioles 2–10 mm. long; rhachis strongly angled or narrowly winged, glabrous or minutely scabrellate on the angles; flowers sessile in small capitula subtended and about equaled by ovate-lanceolate acuminate bracts; perianth subglobose, about 1.5 mm. long, deeply 6-lobed, glabrous, the lobes round-ovate, obtuse, 1-nerved, very thin; stamens 3, the stout filaments about as long as the perianth-tube, divergently branched above, marked with red at the apex, each branch bearing an anther-sac; staminodia 3, slender, Y-shaped, about equaling the filaments; pistillate spikes solitary, axillary, 8 cm. long, narrowly winged, glabrous; bracts linear-subulate, 2.5 mm. long; ovary narrowly fusiform, 4 mm. long, with 3 narrow wings and 3 thick lobes, minutely red-dotted; corolla subglobose, 1 mm. long; styles 3, short, connivent, with divergent stigmas; fruiting spikes becoming 3 dm. long; fruit reflexed, as much as 28 mm. long, the wings semi-obovate-oblong, 9 mm. wide, broadly triangular at apex.

Type, *Hitchcock* 17559, collected at Issorora, Aruka River, lat.  $8^{\circ} 10' N.$ , long.  $59^{\circ} 50' W.$ , and deposited in the herbarium of the New York Botanical Garden.

*D. oblonga* is most closely related to *D. polygonoides* H. & B., from which it is well differentiated by the much longer and more pointed fruit.

*Dioscorea trichanthera* n. sp. Stem about 2 m. long, angulate, glabrous, or minutely puberulent, twining to the right; petioles slender, 45–60 mm. long, mostly glabrous or more or less puberulent near the base and the dorsiventrally flattened apex; leaf-

blades broadly ovate-triangular to ovate-oblong, 55-100 mm. long, 33-58 mm. wide, exclusive of the basal sinus 10-22 mm. deep, thin and membranous, glabrous above, slightly paler beneath and sparsely hirsute with curved, nearly appressed hairs 0.3 mm. long, or varying to nearly glabrous, abruptly narrowed at the apex into a narrowly triangular acumen 4-10 mm. long, sparsely glandular near the base, pellucid-lineate, the basal sinus rounded, the basal lobes broadly rotund; second and third veins arcuately ascending and entering the apex, fourth and fifth divergently spreading and extending one third to one half the length of the blade, sixth and seventh not passing beyond the basal lobes, simple, or in the largest leaves inconspicuously bifid, nearly parallel to the margin; pistillate inflorescence not seen; staminate racemes single in the axils of the upper leaves, unbranched, 10-20 cm. long, the rhachis angled, thinly to rather densely short-villous or subhirsute, floriferous from near the base; pedicels single or paired, 1-2 mm. long, hirsute; bracts 2, ovate, acuminate, glabrous, the lower somewhat the larger and equaling or exceeding the pedicel; perianth-tube very short; perianth-lobes widely spreading, 3 mm. long, 1 mm. wide, rather thick, oblong, acute or obtusish, glabrous within, glabrous or sparsely pilose with a few short hairs without; stamens 6; filaments 2 mm. long, terete below, laterally flattened at the apex, incurved, the basal third adnate to the perianth and twice as thick as the distal two thirds; anther-sacs elliptic, introrse more or less pubescent on the inner face; style-rudiment 1, broadly ovoid, blunt, shallowly 3-lobed.

Type, *Gleason 804*, dry sandhills east of Rockstone, deposited in the herbarium of the New York Botanical Garden. Other sheets referred to this species are *Gleason 67*, Tumatumari; *La Cruz 2190, 2232*, and *Lang 326*, upper Mazaruni River; *Jenman 5800*, Mazaruni River; *Jenman 4736*, Bartica; *La Cruz 2646*, Malali, Demarara River.

The sheets cited show a considerable degree of variation in the length of the pedicel and in the amount of pubescence on the lower leaf-surface, rhachis, pedicel, and anthers, but I have found no definite structural characters upon which to base a division of the species.

The two collections of Jenman have been distributed under the name *D. piperifolia* Willd. Kunth pointed out in his Enumeration in 1850 that this name has been applied to various different species, including *D. polygonoides* H. & B., *Helmia monadelphica* Kunth, and several species of Grisebach's section *Centrostemon*. All of these differ radically from our species in the

structure and position of the stamens or the shape of the perianth. Our species finds its proper position in Grisebach's section *Epistemon*, near the Brazilian *D. dodecaneura* Vell. Among the species of this section, it is distinguished by its pubescent, glandular, punctate-lineate leaves, its simple, pubescent racemes, and its pubescent anthers.

*Dioscorea megacarpa* n. nom. (*Dioscorea truncata* "Miq.," Schomb. Faun. & Fl. Brit. Guiana 899. *Nomen nudum*. 1848. *Dioscorea truncata* Prain, Kew Bull. 1916: 194. 1916. Not *D. truncata* Miq. Linnaea 18: 23. 1844.)

It is probable that the nomenclatorial confusion which has surrounded this species is due to a peculiar oversight in the Index Kewensis, which omitted all reference to Miquel's species of 1844. Miquel's name was applied to *Focke 618*, from Surinam, a plant with deeply 5-lobed leaves, regarded by Pulle as not distinct from *D. trifida* L. f. The name was erroneously applied by Schomburgk to his number 224, but without description. The description was supplied, and the name first validly published in this sense, in 1916 by Sir David Prain, who also gave a full history of the species and excellent critical notes on its relationships.

The type of *D. megacarpa* remains *Schomburgk 224*, in the herbarium of the Royal Botanic Garden at Kew, where it is also represented by *Sagot 860* and *Jenman 1701*. To these may now be added two collections from British Guiana of more recent date, *La Cruz 2123*, from the upper Mazaruni River, and *La Cruz 3380*, from the Barima River, lat. 8° 20' N., long. 59° 50' W. The former exhibits mature fruit of the typical oblong-obovate shape and as large as 50 by 27 mm.

It may be noted that a still more recent use of the name *D. truncata* by Dr. H. H. Rusby for a Colombian species is of course invalid.

*Vernonia trichoclada* n. sp. *Lepidaploa scorpioideae foliatae*; plants gregarious, 12 dm. high, herbaceous or suffrutescent; stem ascending or erect, simple to the inflorescence, nearly terete, densely and persistently clothed with pale brown, spreading or somewhat deflexed hairs 1.5–2 mm. long, the internodes mostly 4–6 cm. long; petioles 5–7 mm. long, pubescent like the stem; leaf-blades thin, narrowly oblong-elliptic, 10–11 cm. long by 28–30 (rarely 34) mm. wide, gradually tapering or subacuminate to the apex, broadest at or slightly below the middle, broadly

cuneate to the base, entire, above rugose with impressed veins, papillose-pubescent on the surface and densely so on the midvein with hairs as much as 1 mm. long, beneath densely pubescent along the midvein with hairs like those of the stem and softly pubescent on the surface with similar hairs 1-1.5 mm. long; lateral veins about 7 mm. apart, diverging at an angle of 70°, the veinlets conspicuously elevated and reticulate beneath the pubescence; inflorescence a sparsely branched panicle, 30 cm. high, 25 cm. broad as pressed, the branches pubescent like the stem, subtended by rameal leaves resembling the cauline and half as long, the internodes below the heads 5-7 cm. long; heads sessile, more or less secund, solitary, or the lower on each branch paired, separated by internodes 3 cm. long below, gradually reduced to 1 cm. above, or the uppermost heads approximate; bracteal leaves subtending paired heads resembling the cauline in shape, but 3-2 cm. long, those subtending single heads linear or linear-lanceolate, 12-6 mm. long; involucre campanulate, 9 mm. high; involucral scales about 45, loosely imbricate, appressed at the base or the covered portion, all but the innermost irregularly curved-spreading or squarrose above, the outer linear-subulate, 3-4 mm. long, aristate, glabrous within, pubescent without with gray hairs nearly 1 mm. long, the middle narrowly ovate-triangular at base, acuminate from near the base to an awn one-half as long as the scale, villous, the inner narrowly ovate-lanceolate, broadest at one-third of their length, long-acuminate to an awn 1 mm. long, thinly villous, the innermost 6-8 scales ovate-lanceolate, not awned, 8 mm. long, appressed-pubescent; achenes 11, 2 mm. long (immature), densely pubescent with ascending hairs; paleae 25-30, linear-oblong, 0.7-0.8 mm. long, minutely pubescent and fimbriate-ciliate; bristles about 65, brown, slender, minutely pubescent, 6 mm. long; corolla white, the slender tube 2.7 mm. long, 0.6 mm. wide at the throat, the lobes linear-oblong, 2.8 mm. long, 0.5 mm. wide, acute, minutely pubescent at the apex; anthers linear, 2.1 mm. long, the basal appendages narrowly triangular, acute, 0.4 mm. long.

Type, *Macbride 5775*, collected at the Hacienda Schunke, La Merced, Peru, alt. about 4000 feet, Aug. 27-Sept. 1, 1923, and deposited in the herbarium of the Field Museum (duplicate in herb. New York Botanical Garden).

*V. trichoclada* appears most closely related to *V. mapirensis* Gleason, of and resembles it very closely in general habit and leaf-form. It differs, however, in its more densely pubescent stem with reflexed hairs, in the quantity and kind of leaf-pubescence, in the larger, more villous involucre, in its squarrose scales with longer aristae, and in the smaller number of flowers in each head.

**Vernonia flexipappa** n. sp. Stems and branches closely and densely pubescent when young with dark brown hairs, becoming glabrous with age; petioles slender, closely pubescent, 5 mm., long; leaf-blades firm, lance-oblong, 50 mm. long, 15 mm. wide, or the upper smaller, broadest near the middle, sharply acuminate at both ends, entire, minutely puberulent above, becoming glabrous in age, somewhat revolute, silvery beneath with close, very fine tomentum, through which appear appressed brown hairs 0.3 mm. long, veins obscure above, the laterals prominent beneath, about 6 pairs, arising at an angle of  $45^{\circ}$  and gently curved-ascending, the veinlets concealed; heads 1-flowered, sessile, closely crowded in a terminal, freely branched cluster 5-10 cm. across as pressed and leafless, except at the base of the principal branches; involucre narrowly campanulate, 5 mm. high, its scales about 10, deciduous, regularly appressed and imbricate, strongly curved around the achene, thinly pubescent on the back, the outermost 2.5 mm. long, obtuse, the inner progressively longer and sharper, the longest 4.5 mm. long, 1.3 mm. wide; corolla-tube terete, 2.7 mm. long, 0.5 mm. in diameter, its lobes linear-oblong, acutish, 2.7 mm. long, 0.5 mm. wide; anthers vernonioid, 3 mm. long, including the basal and apical appendages; pappus-bristles pale tawny, 7 mm. long, about 50, fragile and easily detached, with a prominent U-shaped curve about 1 mm. from the tip; a few outer bristles one-half to one-third as long, straight and slender; achenes 2.5 mm. long, dark brown, nearly terete, minutely resinous.

Type, *André 2250*, collected at Loja, Ecuador, and deposited in the herbarium of the New York Botanical Garden. A second sheet in the same herbarium is *André K 1152*, labeled "Loja-Zamora, 1876." The species evidently belongs to the section *Critoniopsis*, as shown by its 1-flowered heads, its deciduous involucre scales, and essentially uniseriate pappus.

**Vernonia trilectorum** n. sp. Stem shrubby, finely striate, very densely and closely short-pubescent or subvelutinous with dull brown hairs, the same integument covering the inflorescence, petioles, and principal veins of the leaves; petioles slender, about 10 mm. long; leaf-blades firm, dark green, elliptic-oblong, 9-11 cm. long, 4-5 cm. wide, broadest near the middle, broadly cuneate at base, entire, tapering regularly to a subacuminate tip, upper surface very thinly pubescent with brownish, slender, appressed or ascending hairs 0.1-0.2 mm. long, set 0.1-0.2 mm. apart, becoming nearly or quite glabrous in age, lower surface similarly pubescent, especially along the veins and veinlets; lateral veins conspicuous beneath, 6-9 mm. apart, arising at an angle of  $60^{\circ}$ , gently curved-ascending, the veinlets reticulate; rameal leaves subtending the principal branches of the inflores-

cence similar, but smaller and narrower, the uppermost only 4 by 20 mm.; inflorescence a freely branched corymbiform cluster, 2 dm. in diameter as pressed; heads 21-flowered, sessile, bractless, 3-5 mm. apart, or the lower more distant; involucre campanulate, 4.5 mm. high; scales about 45, erect or the outer barely spreading when pressed, loosely imbricate, the outermost narrowly triangular-subulate, 1 mm. long, prominently carinate, densely villous throughout, the inner progressively longer, carinate only at the apex, the innermost narrowly lance-oblong, acuminate, not carinate, thinly pubescent; corolla pink, the tube relatively stout, scarcely ampliate, 3 mm. long, the lobes erect, acute, narrowly triangular, 1.6 mm. long; anthers 2.3 mm. long; style-branches slender, tapering, pubescent externally; achenes 2 mm. long, strongly angled, pale brown, densely sericeous with white ascending hairs about 0.2 mm. long; pappus dull brown, the bristles fragile, 4.5 mm. long, slender, rather prominently pubescent, the paleae linear-oblong, 0.5-0.6 mm. long, conspicuously ciliate-fimbriate.

Type, *Pennell, Killip, & Hazen 8556*, collected in thickets at Cuchilla, east of Zarzal, Dept. El Valle, Colombia, alt. 1200-1600 m., 22 July 1922, and deposited in the herbarium of the New York Botanical Garden. Other collections from El Valle are *Pennell, Killip, & Hazen 8555*, same place and date as the type, *Pennell, Killip, & Hazen 8499*, open valley, Quebrada Nueva to Cuchilla, alt. 1100-1300 m., 21, 22 July, 1922, and *Killip 11,232*, woods along stream, "Calima," on Rio Calima, 14, 15 Sept., 1922;—Dept. Caldas: *Pennell, Killip, & Hazen 8692*, stream-bank, Rio Quindio, above Armenia, alt. 1300-1500 m., 25 July 1922;—Dept. El Cauca: *Pennell & Killip 6378*, thicket growth ("machimbi"), Cuatro Esquinas to Rio Piendamó, alt. 1700-1900 m., 6 June 1922, *Killip 6892*, woodland, Coconuco to Popayan, alt. 2000-2500 m., 18 June 1922, *Pennell & Killip 7248*, oak grove, east of Rio Ortega, alt. 1600-1700 m., 27 June 1922, and *Pennell & Killip 8075*, woodland, Rio Ortega to "El Ramal," alt. 1900-2200 m., 2 July 1922.

The description above has been drawn from the type exclusively. Of the other eight specimens, five agree with the type in all essential features, differing only in minor matters, such as the size of the inflorescence and the dimensions of the leaves. In *6892* and *8075*, the paleae are linear and 1 mm. long. In *8555* and *8075*, the leaves are persistently softly pubescent beneath with slender hairs 0.7 mm. long.

*Vernonia Pennellii* n. sp. Stem and branches terete, finely



striate, densely and softly pubescent or almost velutinous with olive-brown hairs; petioles 12 mm. long, pubescent like the stem; leaf-blades thin, dull green, narrowly ovate-oblong, obtuse or broadly acute at base, entire, gradually narrowed from below the middle to a subacuminate tip, the upper surface very thinly and softly papillose-villous when young, becoming glabrous and rugose at maturity, the lower surface permanently softly villous with very slender hairs 1-1.5 mm. long, lateral veins impressed above, prominent beneath, from 5 mm. apart near the base to 15 mm. toward the apex, ascending at an angle of 60°, gently curved, extending almost to the margin, the veinlets prominently reticulate; inflorescence terminal and from the upper axils, compound, freely and repeatedly branched, 20 cm. wide as pressed, the axes more or less zigzag, the internodes successively shorter distally, the nodes normally bearing 1 terminal head and 2 sympodial branches or 2 heads of different age and 1 sympodial branch; heads very numerous, sessile, 9-flowered; involucre 12 mm. high, its scales about 24, all straight, erect, long-acuminate, loosely imbricate, somewhat spreading when pressed, the outermost narrowly triangular, pubescent, 2 mm. long, the inner linear-oblong or linear-lanceolate, pubescent on the exposed surface, densely so toward the apex, the innermost 11 mm. long, 2 mm. wide; corolla glabrous, pale pink, the tube 6 mm. long, gradually expanded above the middle to 0.8 mm. in diameter at the throat, the lobes linear-oblong, 3.3 mm. long; anthers 3.7 mm. long, including the basal and apical appendages; style-branches 2.5 mm. long, gradually tapering, pubescent externally; achenes (immature ?) stout, 1.6 mm. long, densely sericeous; pappus white, the paleae about 15, 1.8 mm. long, 0.2 mm. wide, acuminate, minutely 1-nerved and ciliolate, the bristles about 60, strongly flattened, somewhat twisted, minutely pubescent, 8 mm. long, 0.1 mm. wide.

Type, *Pennell 2642*, collected in a clearing on a bushy slope, Tequendama, Dept. Cundimarca, Colombia, alt. 2500-2700 m., 28 Oct. 1917, and deposited in the herbarium of the New York Botanical Garden. The specimen consists of two floriferous branches from a shrubby vine. The largest leaf subtends a lower branch of the inflorescence and measures 170 by 55 mm.; the next leaf above it is 145 by 48 mm., and the upper bracteal leaves are much reduced. The species bears no resemblance to any of the other Colombian species known to me.

*Vernonia spinulosa* n. sp. Stem herbaceous, finely striate, minutely villous above, becoming glabrous below, simple at the base, with several straight, leafy, ascending, floriferous, axillary branches above, the internodes 2-3 cm. long; petiole none or not exceeding 1 mm. in length and tomentose; leaf-blades thick

and firm, lanceolate, 35-40 mm. long, 7-9 mm. wide, long-acuminate to a sharp subulate tip, entire and frequently somewhat revolute, abruptly rounded at base, upper surface dull green, somewhat rugose, pubescent when young, persistently scabrellate with the papillose hair-bases at maturity, lower surface dull gray, densely tomentulose and dotted with elevated black glands; lateral veins mostly 5 or 6 pairs, impressed above, inconspicuous beneath, ascending at an angle of  $45^{\circ}$ ; inflorescence not differentiated; heads 6-flowered, sessile, solitary or occasionally paired, erect or strongly ascending, partly axillary, partly supra-axillary 2-5 mm. above the node; involucre narrowly fusiform, 10-12 mm. high, 3 mm. in diameter; involucre scales about 14, appressed at base, curved-spreading and acuminate into a stiff spinulose apex, sparsely pubescent and ciliate on the exposed portion, glabrous on the covered base and inner surface, the outer lance-subulate, 6 mm. long, acuminate from below the middle, the inner progressively longer and oblong; receptacle with an annular elevation bearing 5 flowers and a central depression with a single flower, glabrous; achenes linear-fusiform, 4 mm. long, shallowly 10-ribbed, with a yellow cartilaginous base, densely hirtellous on the body with ascending hairs 0.3 mm. long; pappus biseriate, the outer paleae about 20, linear, 1-1.3 mm. long, contiguous at base, acuminate, finely pubescent on the outer surface, the inner bristles straight, slender, smooth, pale tawny, 6.5 mm. long, minutely clavate at the apex.

Type, *Pennell 4066*, collected in a thicket at Sincelejo, Dept. Bolivar, Colombia, Jan. 26, 1918, alt. 250-350 m., and deposited in the herbarium of the New York Botanical Garden.

The type specimen exhibits the top of a branching herbaceous plant, devoid of branches for 25 cm., and bearing 5 straight floriferous branches above, each 10-25 cm. long. Heads are developed at the base of all the rameal leaves and also on the opposite side of the axis, at a distance above the axil equal to one third of the internode. Later accessory heads also appear in the axils, but none has reached maturity in the type. The corollas were noted by the collector as red-violet in color, but, like many other species of the genus, the flowers have continued their development after collection and most heads contain only mature achenes. In the few cases where the corollas have persisted, the tube is slender, 4.5 mm. long, not ampliate above, and glabrous; the lobes and stamens have in every case been broken off, but the lobes were apparently minutely pubescent without.

A second sheet, *Pennell 4015*, from similar altitudes at Buena-

Vista, east of Sincé, Bolivar, is fragmentary, but exhibits a few leaves on the basal portion of the stem. These are much broader than the rameal leaves of the type, and as much as 75 by 32 mm. in size.

*Vernonia spinulosa* is a member of the section *Stenocephalum*, and is most closely related to *V. jucunda* Gleason, of Chiapas, Mexico. It is distinguished from the latter by its narrow rameal leaves, its thinner indument, its larger involucre, achenes, and pappus, and the position of the heads.

*Vernonia trichotoma* n. sp. Arborescent, 6 m. tall; branches 8-angled, closely ferruginous-tomentose when young, terete and persistently but very thinly tomentulose in age; leaves opposite; petioles 10-14 mm. long, slender, channeled above, tomentulose; blades firm, oblong-lanceolate, 9-12 cm. long, 23-32 mm. wide, broadest near the middle, frequently somewhat falcate, tapering regularly to a blunt tip, entire, long-cuneate to the base, upper surface dark green, glabrous, shining, with finely reticulate, elevated veinlets, lower surface pale brown, densely and softly tomentose, the veinlets obscure; lateral veins diverging at an angle of  $45^{\circ}$ , strongly curved-ascending, the lower 2-3 mm. apart, the upper progressively wider spaced to 13-20 mm.; inflorescence a compact, terminal, trichotomous, corymbiform cyme, 10 cm. wide as pressed, the lower branches subtended by foliage leaves, the upper bractless (one small bracteal leaf on the type), all closely tomentose; heads 11-flowered, on pedicels 3-7 mm. long; involucre campanulate, 8 mm. high, its scales about 20, closely and regularly imbricate in  $3/8$  phyllotaxy, erect, obtuse or rounded at the dark tip, densely villous without, sparsely villous within, the outermost minute, the outer broadly ovate, 2 mm. wide, the inner progressively longer and narrower, the innermost linear, 7 mm. long, 1 mm. wide; corolla white, the tube slender, terete, not ampliate above, 3.3 mm. long, 0.5 mm. in diameter, the limb campanulate, the lobes divergently spreading and then curved-ascending, 3.5 mm. long, 0.7 mm. wide, narrowly elliptic-oblong, somewhat constricted above the base, prominently revolute, tapering to the acute apex, villous externally near the tip with hairs 0.3 mm. long; filaments flat, inserted on the throat of the corolla, glabrous; anther-tube pentagonal, 3 mm. long, glabrous, the 5 basal appendages triangular, 0.3 mm. long, the tips ovate-triangular, obtuse, 0.7 mm. long; style branches spreading, filiform, 2 mm. long, pubescent without, channeled within; achenes (immature) 10-angled, dark brown, 3.6 mm. long, minutely glandular; pappus biseriate, the inner bristles pale-tawny, 6.5 mm. long, minutely pubescent, the outer paleae similar, but only 2 mm. long.

Type, *Pennell & Killip 6584*, collected in the forest at "Canaan," Mt. Purace, Dept. El Cauca, Colombia, alt. 3100-3300 m., June 11-13, 1922, and deposited in the herbarium of the New York Botanical Garden.

In general habit, this species is reminiscent of *Critoniopsis Lindenii* Sch.-Bip., but differs in its much larger heads with 11 flowers. It probably belongs to the section *Critoniopsis*, but in its present condition shows no evidence of deciduous involucre scales.

*Rapatea linearis* n. sp. Acaulescent; leaves narrowly linear, 1 m. long, 10-12 mm. wide, bright green, glabrous; peduncle erect, 1 m. high, glabrous, flattened and prominently winged, increasing in width to nearly 1 cm. at the summit; bracts 2, reflexed, narrowly triangular, 7-11 cm. long, 2-3 cm. wide at the cordate base, tapering regularly to the acute apex, green, glabrous; head depressed-globose, 3-5 cm. in diameter, densely many-flowered; pedicels 3 mm. long, glabrous; bractlets about 14, spirally imbricate, ovate-oblong, the outer 5 mm., the inner 15 mm. long, glabrous, 3-7-nerved, the lower half appressed from the broad base and scarious, the upper half green, outwardly curved and prominently spreading, long-acuminate into a subulate tip minutely spotted with purple; sepals 3, 7-nerved, 16 mm. long, united into a tube and very thin and transparent for 6 mm., the distal 10 mm. stiff, coriaceous, glabrous, yellowish-green, narrowly triangular-lanceolate, tapering to a convolute subulate tip, spreading at anthesis; corolla-tube 10 mm. long, very thin and transparent, faintly nerved; petals 3, yellow, membranous, ovate, 12 mm. long, 7 mm. wide, abruptly acuminate into a short tip, widely spreading at anthesis; stamens 6, inserted on the corolla-tube 1.5 mm. below its summit; filaments transparent, 1.5 mm. long, incurved and then erect; anthers linear-subulate, 5 mm. long, cordate at base, 2-celled, white below, tapering into a gently curved, yellowish-brown appendage, marked with a central, introrse, elongate cleft expanding at its base into a circular pore; ovary subglobose, 3 mm. in diameter; style slender, 14 mm. long.

Type, *La Cruz 3931*, collected along the Wanama River, Northwest District, British Guiana, and deposited in the herbarium of the New York Botanical Garden; a second collection is *La Cruz 4293*, from Assakatta, Northwest District.

Easily distinguished from *R. paludosa* Aubl., the common species of the Guianas, by its narrower leaves, shorter pedicels, and narrower, regularly tapering bracts.

**Bihai sylvestris** n. sp. Stems erect, 12 dm. high; leaf-sheaths glabrous; petiole of the uppermost leaf 5–20 mm. long, of the second leaf 20–50 mm., glabrous; leaf-blades green and glabrous on both surfaces, narrowly lanceolate, 25–51 cm. long, 3–8.5 cm. wide, long-acuminate, rounded or subcordate at the base; peduncle exserted 11–33 cm. beyond the uppermost leaf, straight, erect, glabrous or somewhat glaucous distally; bracts 5 or 6, widely spreading, linear, straight, glabrous, conspicuously glaucous, the lowest 13–18 cm. long and sometimes expanded at the apex into a flat, lanceolate-oblong lamina, the upper uniformly reduced in length to 2–3 cm.; rhachis flexuous, glabrous, glaucous, the internodes 3–4 cm. long or the uppermost shorter; bracteoles glabrous, scarious, brown, 15–20 mm. long; flowers 5–10 in each bract, on glabrous pedicels 1–2 cm. long; corolla scarlet, 5 cm. long.

The herbarium of the New York Botanical Garden contains five specimens, all from forests or thickets at Tumatumari, British Guiana: *Gleason* 5, 82, 105 (type), and 937, and *Hitchcock* 17,347.

*Bihai sylvestris* seems to be most closely related to *B. acuminata* (Rich.) Kuntze, a common species in British Guiana, but differs from it and from the other species of the region in its shorter petioles, narrower leaf-blades broadly rounded at the base, and heavily glaucous bracts.

**Renealmia pedicellaris** n. sp. Sterile stems 12–15 dm. high, 1 cm. in diameter, plagiotropic; leaf-sheaths strongly striate, somewhat reticulate, scabrellate on the ribs, the ligule rounded, 2 mm. long, pilose with brown hairs; leaf-blade oblanceolate, 48 cm. long, 8.5 cm. wide, abruptly acuminate, somewhat cartilaginous on the margin, tapering to an unsymmetrical base, glabrous on the surface, the short petiole (1 cm. long) and lower part of the midvein more or less pubescent; flowering stems prostrate, 4–8 dm. long, the lower half sterile, bracteate, the bracts oblong, sheathing, covering two-thirds of each node, glabrate below, pubescent at the tip; panicle narrowly oblong, the bracts, bractlets, rhachis, and pedicels pubescent; flower-clusters about 1 cm. apart, 3–5-flowered; common pedicel 3–6 mm. long; pedicels 1–3 cm. long, thickened distally, 3–5 mm. apart; fruit subglobose, blue-black, 10 mm. in diameter, strongly nerved, puberulent when young, becoming glabrous with age, 9-seeded, each three seeds surrounded by a scarious aril; seeds brown, 3 mm. in diameter, calyx persistent, campanulate, 4–5 mm. long, puberulent to glabrous, irregularly torn or with several short terminal teeth.

Type, *Gleason* 138, collected in dense upland forest, Tumatumari, British Guiana, and deposited in the herbarium of the

New York Botanical Garden. The bracts have mostly disappeared, but are apparently linear-lanceolate and about 15–20 mm. long. The bractlets are of the same shape, about 10 mm. long, and much surpassed by the unusually long pedicels.

*Renealmia pedicellaris* is apparently related to *R. occidentalis* (Swartz) Sweet and to *R. orinocensis* Rusby. From the former it differs in having fewer flowers in a cluster, on much longer pedicels; from the latter in its much shorter clusters. It may be still more closely related to *R. floribunda* K. Schum., and closely resembles the plate of that species in Flora Brasiliensis under the name *R. occidentalis* var. *longipes* Peters., but differs in its larger panicles and fruit and in its much more copious pubescence.

*Renealmia pilosa* n. sp. Sterile plant 10–15 dm. high, with 10–15 alternate leaves; leaf-sheath glabrous, striate, the ligular lobes truncate or rounded, 2 mm. wide, pubescent externally; leaf-blades sessile or on petioles 3–10 mm. long, oblong-lanceolate, 51 cm. long by 8 cm. wide, or smaller, abruptly acuminate, scarious on the margin, tapering at base, glabrous; flowering stems more than 4 dm. long; peduncle glabrous or finely and sparsely pilose, covered with erect, appressed, sheathing scales which are 10 cm. long, minutely pilose basally, and glabrous toward the apex; panicle 25 cm. long, the rhachis finely pilose; bracts narrowly linear-lanceolate, obtuse, pilose externally near the base, otherwise glabrous, the lower as much as 5 cm. long, the upper gradually reduced, the uppermost only 1 cm. long; clusters mostly 2–3-flowered, on a pilose common pedicel 3–10 mm. long; bractlets broadly ovate-campanulate, 1 cm. long, pilose on the back near the base; pedicels 5–10 mm. long, nearly glabrous; ovary broadly ellipsoid, glabrous, 5 mm. long; calyx turbinate-campanulate, 6 mm. long, with 3 rounded lobes, pilose near the base, pubescent or subtomentose at the apex.

Type, *H. H. Smith* 2318, collected at Don Amo, Santa Marta, Colombia, altitude 1600 feet, and deposited in the herbarium of the New York Botanical Garden. The collector notes that it is local in damp thickets and produces yellow flowers in June, followed by red berries turning black at maturity and with a strong fruity odor. *André* 2014, from Ibagué, and *Pennell, Killip, and Hazen* 8513, from Cuchilla, Department of El Valle, may also be referred here.

*Renealmia pilosa* is obviously of Schumann's series Scaposae, subseries Paniculatae, although the basal location of the inflorescence is not shown on the three specimens cited. Within

this group, it is related to the Antillean *R. occidentalis* (Swartz) Sweet, and apparently also to the Colombian *R. Lehmannii* K. Schum., which I have not seen. It differs from the former in its few-flowered clusters, and from the latter, according to Schumann's careful description, in the conspicuous pilose pubescence of the rhachis, pedicels, bracts, and calyx.

*Ischnosiphon foliosus* n. sp. Stem 6-9 dm. high, simple, leafless below, bearing leaf-scars above and at the summit about 8 crowded leaves separated by internodes 3-4 mm. long; leaf-sheaths 7-10 cm. long, glabrous, the membranous margins 3 mm. wide, tapering to the apex, not auriculate; petioles 11-40 mm. long, the basal portion strongly angled, glabrous, the distal 7-14 mm. somewhat swollen, terete, minutely roughened; leaf-blades ovate-lanceolate, 11-16 cm. long, 3.5-6.5 cm. wide, obtuse or rounded at the base, abruptly short-acuminate, the point somewhat excentric to the right, glabrous on both sides, midvein extending three-fourths the length of the blade, the lateral veins strongly ascending; inflorescence single from the upper axils; peduncle 8 cm. long, erect, strongly angled, glabrous; spikes 2, 7-12 cm. long, terete or nearly so; bracts appressed, cymbiform, embracing the rhachis, ovate, 30-35 mm. long, acuminate, separated by internodes 10-13 mm. long, finely striate, glabrous; first and second bractlets linear-oblong, the third filiform, clavate-thickened at the apex, all 3 cm. long and equaling the linear glabrous sepals; capsule oblong-obovoid, 2 cm. long, villous, especially at the summit.

Type, *Gleason 721*, collected in dense upland forest, Tumatumari, British Guiana, and deposited in the herbarium of the New York Botanical Garden; also *Gleason 176*, from the same locality.

In several respects this species is remarkable in comparison with the other species of the genus. In its closely crowded and regularly distichous leaves it approaches *I. Martianus*, the only species hitherto described with such an arrangement. It differs from it in its petiole, which is callously thickened only at the summit, in its glabrous bracts, and in its proportionately wider and shorter leaves. In my dissections I have found but a single flower for each bract; if this character is constant, it is unique for the family Marantaceae.

AFRAMOMUM MELAGUETA (Rosc.) K. Schum. (*Amomum melagueta* Rosc.). The type locality for this African species is British Guiana, whence specimens were sent by Parker a century ago. Recent collections (*La Cruz 1148, 1250, 3310, 3327, 4034*)

show that it is still widespread and perhaps naturalized in that country.

*CALATHEA CYCLOPHORA* Baker. This species, based on *Appun* 252, from British Guiana, is represented in recent collections by *Hitchcock* 17,321 and *Gleason* 577 from Rockstone, *La Cruz* 1522 from the Rupununi region, *Lang* 245 from the upper Mazaruni river, and *La Cruz* 2913, 3127, and 3658 from the northwestern coastal region. Schumann erroneously refers it to Mexico in his treatment of the genus in the *Pflanzenreich*.

*Dupatya roraimae* (Oliver) n. comb.

*Paepalanthus roraimae* Oliver, Trans. Linn. Soc. II. 2: 286. pl. 49 B, f. 7-14. 1887.

*Dupata Karstenii* (Ruhl.) n. comb.

*Paepalanthus Karstenii* Ruhl., *Pflanzenreich* 4<sup>30</sup>: 155. 1903.

*Pennell* 2256 and 2685A, from paramos near Bogota, Colombia, have been tentatively referred to this species.

*DUPATYA PILOSA* (H. B. K.) Kuntze. *Holton* 122, collected near Bogota, was referred to this species by Hochreutiner, and *Pennell* 1997, from the same vicinity, seems to be the same in all essential respects. *Pennell* 2074, also from paramos near Bogota, has shorter, more rigid, and more densely pilose leaves, bracts 3 mm. long, and petals of the pistillate flower oblong-ob lanceolate and fully 2 mm. long. In the two sheets of *D. pilosa* cited above, the bracts are only 2 mm. long and proportionately much broader and the petals are broadly triangular-dilated above the narrow oblong base. *Pennell*'s specimen may represent an undescribed species, but should be compared with Humboldt's types before any final conclusion is reached.

The genus *Gnetum* is represented in recent collections of La Cruz by three numbers, illustrating three distinct species, of which one is hitherto undescribed. They may be separated as follows:

Veinlets (examined by transmitted light) conspicuously reticulate, the areoles 0.2-0.3 mm. in diameter; leaves elliptic, broadest near the middle, broadly obtuse at base, rounded to an apiculate apex (*La Cruz* 4311)... *G. paniculatum* Spruce  
Veinlets indistinct, not reticulate; leaves of an ovate type, broadest below the middle, more gradually tapering to an acute or abruptly acuminate apex.



Leaves elliptic-ovate, twice as long as wide, rounded at base; axis of the staminate inflorescence slender, not swollen immediately above the insertion of the sporophylls (*La Cruz 3522*) . . . . . *G. nodiflorum* Brongn.

Leaves broadly ovate or subrotund, a third to a half longer than wide, broadly rounded or subcordate to an abruptly short-cuneate base; axis of the staminate inflorescence prominently swollen immediately above the insertion of the sporophylls, the latter borne on a horizontal disc (*La Cruz 4222*) *G. Cruzianum*

**Gnetum Cruzianum** n. sp. Stems woody, climbing 6 m.; petioles stout, 10–12 mm. long, strongly bicarinate above; leaf-blades broadly ovate or subrotund, as large as 13 cm. long by 11 cm. wide, coriaceous, dull-green above, brown-green beneath, glabrous, gradually rounded from below the middle to a subacuminate or triangular-apiculate apex, broadly rounded or subcordate below to a short-cuneate base; lateral veins 4 or 5 pairs, ascending at an angle of 45 degrees, faintly arcuate and anastomosing at two-thirds of the distance to the margin; secondary veins faint, barely impressed above, irregularly anastomosing, almost invisible on the lower surface; veinlets indistinct; staminate inflorescence paired in the upper axils, simple or sparingly branched, 10–15 cm. long, flexuous, the nodes 10–20 mm. long; involucre hemispherical, 5 mm. in diameter; internodes sterile and densely villous within the involucre on the basal 2 mm., then expanded into a spreading, subhorizontal, floriferous disc 3 mm. in diameter, strongly swollen and tomentose immediately above the disc.

Type, *La Cruz 4222*, collected at Kamakusa, on the upper Mazaruni River, British Guiana, and deposited in the herbarium of the New York Botanical Garden. The swollen portion of each floriferous internode, with its accompanying tomentum, is visible above the sporophylls.

## A study of progressive cell plate formation\*

BESSIE GOLDSTEIN

(WITH ELEVEN TEXT FIGURES AND PLATE 6)

In connection with a study of the cells of the meristem and protoderm of the growing tips of healthy tobacco plants and those affected with mosaic disease, I have had occasion to study division figures in cells which are already more or less vacuolated.

Treub (23) seems to have been the first to point out the peculiarities of cell division in large vacuolated cells having a very thin parietal layer of cytoplasm, the primordial utricle. His figures show clearly that nuclear division and cell division are distinct processes in the life of the cell. He points out too that cell plate formation is a progressive process and that the cell plate widens gradually thus cutting across the cell protoplast and dividing it into two. Only when the cell plate reaches the walls of the mother cell, are there two distinctly separated daughter cells.

Stages in the formation of the cell plate have been figured in many studies of cytokinesis, but these figures have generally represented a side or lateral view of the division figure. This is because the material is generally cut longitudinally, and the sections presented views perpendicular to the cell plate. Cross sections of growing tips presenting polar views of cells in division stages in my material, show the cell plate development in aspects which, as will be, noted later, are easily misinterpreted. Rings of kinoplasmic material appear to encircle two nuclei which often can be seen lying more or less directly over one another, or overlapping. Sometimes it is necessary to focus carefully to distinguish the fact that there are two nuclei present. This gives the appearance of a binucleate cell with a halo. The ring or halo of granular or fibrillar material is the phragmoplast or fibrillar complex seen in polar view.

Such polar views of late cell plate formation were figured by Went (24) in cells of the endosperm of *Fritillaria imperialis*. In his *plate 11, fig. 17*, a cell division figure in polar view, shows

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\* Contributions from the Department of Botany of Columbia University, no. 338.

the kinoplasmic fibrillar ring with a single nucleus. In *fig. 18*, the fibrillar complex has become separated into two arcs as a result of the fusion of the lateral portions of the ring with the walls of the mother cell. Strasburger (19) also shows an excellent polar view of cell plate formation in an endosperm cell of *Fritillaria imperialis*. This is in *plate 2, fig. 20*, where the ring of kinoplasmic fibrils lies in a large polygonal cell, and a single nucleus only is present in the section. Némec (12) shows several polar views (*figs. 15, 17*) of early stages in cell plate formation in the cells of the wound periderm of the potato tuber.

Pranker (14) records the occurrence of multinucleate cells in various undifferentiated tissues of immature vegetative organs, and believes the many nuclei arise by amitosis.

Beer and Arber (4) from their studies of growing tissues in a large number of plants, conclude that the occurrence of multinucleate and binucleate cells is very common, and that the many nuclei arise in all cases by means of mitotic division. They ascribe the binucleate condition to certain peculiarities of cell division, by which a so-called phragmosphere may cut off a central cell containing two or more nuclei from a bounding cell, the remainder of the mother cell, which has no nuclei.

My own observations show clearly that in the case of the growing tips of tobacco plants, no such binucleate cells are formed, and that cell division in every case proceeds quite normally. The report of binucleate cells and the peculiarities of cell division referred to are the result of a failure to take into account the appearance of ordinary cell division figures when seen in polar view or when oblique to the plane of the section, and also apparently a failure to focus carefully in order to determine the correct relative position of the young daughter nuclei.

The multinucleate condition in which great numbers of nuclei are seen in a single cell should not be associated at all with the supposedly binucleate condition discussed by Beer and Arber. The problem as to what this multinucleate condition signifies and why it is found in the cells of the plants studied certainly needs careful investigation.

Bailey's (1) statement in regard to multinucleate cells commonly believed to be present in such elongated cells as the cambium initials, shows that the apparently multinucleate condition in such cases, may simply be due to a failure of the

observer to realize that the thickness of the section may include parts lying at entirely different levels and in different cells. He states that in tangential, longitudinal sections of the cambium, the elongated initials frequently appear to be multinucleate, due to the fact that several radially flattened cells are exactly superimposed so that their nuclei lie quite close to the same focal plane.

Hutchinson (8, 9) finds that in the pollen grains of *Abies* and *Picea* the mitotic division of the central or primary cell nucleus is not followed by the ordinary cell plate formation, but by what he calls a form of free cell formation. The generative nucleus becomes enclosed in a hollow cylinder of fibers, the remains of the central spindle, which fuse lengthwise side by side, cutting the generative cell out of the primary cell, and leaving the tube nucleus in the cytoplasm of the original primary cell. In the light of my studies however, it seems to me that his figures show that cell plate formation is proceeding in the usual way by the formation and thickening of additional fibers at the periphery of the cell plate already formed from the central spindle, and that his claim that free cell formation occurs in these cases has arisen from a failure to interpret correctly polar and oblique views of his division figures.

We have relatively few studies of division figures as they occur in large vacuolated cells where the cytoplasm during the resting stages is found in the form of slender threads and broader strands and films cutting through the protoplasts in all direction. The nucleus may lie suspended anywhere in such a system. Treub's (23) original figures of cell plate formation include cases of division in such large vacuolated cells as those of the ovule cells of *Epipactis palustris*, the fundamental tissue of young flowers of *Iris pumila*, internodal cells of *Chrysanthemum leucanthemum*, and various other plants. His figures in plate 4 show typical cell plate formation in such cells as seen from the side and as ordinarily figured. Beer and Arber's (4) studies also dealt with cell plate formation in large more or less vacuolated cells, but as noted they seem to have interpreted incorrectly sections cut parallel to the forming cell plate.

In my studies young tips of vigorously growing tobacco plants about eight inches high were cut off from both healthy and mosaic infected specimens. The material was fixed in various

fixing solutions—chromo-acetic, Bouin's solution, Allen's modification of Bouin's method, both hot and cold, Němec's chrom-formalin method, and the different strengths of Flemming's solutions. I find that Allen's modification of the Bouin method, fixed either at 38° C., or even at ordinary room temperature, and Flemming's weak solution are the best for the study of nuclear and cell divisions in this material. Cross and longitudinal sections were cut for study. The sections were cut 10 microns thick and stained with Flemming's triple stain.

I have studied cells of the tip as well as those occurring in the very young leaves or leaf primordia forming below the tip. These cells are characterized by large vacuoles, across which run strands of cytoplasm of varying size and form. A very thin layer of cytoplasm, the primordial utricle, lines the walls. The nucleus may lie against a wall, or hang suspended in the cytoplasmic strands. The plastids are found in the strands of cytoplasm, and stain a deeper orange than the cytoplasm, and when they contain starch, the starch grains are bright blue in the orange plastid. The young cell plate immediately after formation appears blue, while the young cell walls are thin and take a very faint orange stain. Older walls take a deep orange stain.

In cells of the meristem that are about to divide, the cytoplasm seems to be more than ordinarily massed around the nucleus. The plastids are often also grouped in this dense cytoplasmic mass about the nucleus, though a few scattered ones may remain in the primordial utricle. A region of yellow staining granular material is often found around the dividing nucleus, and this may be the source of the kinoplasmic material soon to appear in the division stages. This granular material is often visible around the spindle and at the poles during later division stages. The polar caps appear at the spireme stage, and consist of fibrils grouped in the form of a cone enclosing a clear space within them. I shall not discuss the problems of spindle formation and the anaphases, as my material presents nothing specially significant for these stages.

During the telophases, the two daughter nuclei are reconstructed, the nuclear membrane is formed, the nucleoles appear, and the chromatin is distributed in the form of more or less rounded chromatin bodies resembling very much prochromo-

somes as described by Rosenberg. The daughter nuclei immediately after division present quite a different appearance from the nucleus of a cell in the so-called resting condition. They stain very deeply. The nucleoles if present are very small, and the chromatin, as noted, is in the form of small bodies lying in a less deeply staining nuclear sap.

A casual examination of cross sections of such tobacco tips would suggest that binucleate cells are not infrequent just as Beer and Arber (4) describe them as occurring in some 177 species of plants. More study shows that the two nuclei which appear to be in one cell, are in fact separated by a cell plate which is parallel or almost parallel to the plane of the section and is thus easily overlooked. I have observed this condition very often in my sections cut ten microns thick, where here and there in the section a cell will appear more intensely stained than neighboring cells. The appearance of two nuclei apparently within the boundaries of such a single cell, is confined entirely to these more deeply staining cells, the dividing walls of two superimposed cells both lying within the section.

In the growing tips of stems, we find a terminal meristem, the growing tip itself, made up of very small polygonal cells whose large nuclei nearly fill the cell, and which are dividing rapidly. Below them there is a region of elongating and enlarging cells, containing large vacuoles through which run thin strands of cytoplasm supporting a nucleus which appears small in comparison with the size of the cells. Division figures in abundance are found here also because the shoots are increasing in thickness. Such a region furnishes excellent material for the study of cell plate formation in large vacuolated cells.

In the cells of the growing tip of tobacco, in the early telophases, the central spindle is as usual barrel shaped. It next widens laterally in the ordinary fashion and changes rapidly from barrel to biconvex lens shape (PLATE 6, FIG. 1). The daughter nuclei in the cells of the tobacco meristem follow the apparently shortening fibers toward the cell plate as it is formed so that no clear space is left between the shortened fibers and the nuclei (FIG. 2). With the completion of the cell plate midway between the daughter nuclei the familiar fiber complex still remains.

The fibers at this stage curve toward and may be connected

with the daughter nuclei. As the cell plate increases in diameter, and the fiber complex gradually moves outward in all directions the threads finally lose all connection with the daughter nuclei, as is shown clearly in longitudinal section (FIG. 2).

This figure shows a long thin line (edge view of the cell plate) in the equatorial region between the two daughter nuclei, while at each end of the line, and more or less at right angles to it, appears the familiar mass of fibers with their ends still curved in toward the daughter nuclei. In terms of the kinoplasm theory, division here is by means of a progressively peripheral development of kinoplasmic material which is adding to the cell plate on its periphery, new kinoplasmic fibrillar material appearing continually in a centrifugal direction, on the outside. The cell division then is by a process of centrifugal development of the original so-called central spindle. The nature of this process has been the subject of much discussion. Bailey's (1, 2) very striking discovery that even in the long, thin, and narrow cambial cells this same peripheral spread of a fibrillar system from the region between the daughter nuclei to the extreme ends of the dividing cell occurs, emphasizes most strongly the apparent importance of fibrillar elements in this most important process in cell reproduction.

Bailey (2) describes and figures such cell division stages in the cambium initials: "Fusiform initials, which frequently are several hundred times as long as they are wide, divide longitudinally by an extraordinary extension of the cell plate." In certain Gymnosperms for example, the cambium initials may attain a length of more than 9000 microns. These cells are uninucleate, so that "the working sphere of their nuclei must extend in certain cases for a distance of several thousand microns."

His description of the stages of cytokinesis in these extremely elongated cells agrees in principle with what takes place in vacuolated cells. The central spindle expands marginally by the addition of peripheral fibers which thicken, shorten, and finally fuse to produce the cell plate material. They thus constitute a circular rim of fibrillar kinoplasm which appears as a halo about the portion of the cell plate already formed, when seen in polar view. The ring can only increase in circumference in narrow tangentially cut cells until it intersects the radial walls.

The lateral portions of the ring then disappear as the cell plate in these regions reaches the radial walls, leaving two separate arcs of kinoplastic fibrillae to continue their progressive movement to the farther regions of the cell. They thus extend the cell plate lengthwise through the cell. These two separate kinoplastic arcs, Bailey believes are distinctly characteristic of elongated or perhaps also much flattened cells, and he gives the name kinoplasmosomes to them.

The term phragmoplast to designate the central spindle and its widening out into a fibrillar halo surrounding the cell plate, is rather misleading, since it seems to associate the activity of cell division with such other cell processes as are associated with chloroplasts, leucoplasts, elaioplasts, etc. There is no real functional analogy here to warrant the use of the term plast or body. There is no definite organ of the cell especially concerned with the production of kinoplastic fibrillar material. It is rather a particular period in the life of the cell which is to be characterized. Starting with the prophase of karyokinesis, and proceeding on through cytokinesis, the metabolic activity of the cytoplasm and nucleus are directly concerned with these kinoplastic activities. As will be noted below, the fibers appear in the cytoplasm along the periphery of the cell plate. The daughter nuclei lying close to the plate, and connected by cytoplasmic strands along the cell plate to its peripheral edge, may also be concerned with the production of the fibrillar material.

There is an objection to the term kinoplasmosomes proposed by Bailey (1) to designate the two parts of arcs of the kinoplastic fibrillar ring, which have not yet reached the walls of the mother cell, as figured in his *plate 29, figs. 54, 57, and 58*. Such separated portions of the kinoplastic ring may arise for various reasons such as the irregular shape of the cell, or the position of the dividing nucleus as it may lie on one side or in a corner of a vacuolated cell.

Traub (23) in his study of the formation of the cell plates of cells containing large vacuoles, notes two modifications of the process according to the type of cells concerned. If the nuclear division has taken place in the center of the cell, then the formation of the plate takes place symmetrically and progressively outward in all directions reaching the cell boundary at



all points simultaneously. If, however, the nuclear division has taken place nearer one side of the cell than the other, then the cell plate reaches the nearer side of the mother cell wall first. The remaining oppositely placed portion of the phragmoplast continues its development toward the farther side of the cell. The splitting of the plate and the formation of the cellulose membrane between may take place on the completed side before the fibrillar complex has reached the opposite side (*plate 4, figs. 35, 40, 42, and 43*). In the latter case, Treub observed that the daughter nuclei in living cells (*plate 3, figs. 12a-12h*), may move out along with the moving phragmoplast across the cell, thus giving evidence of their direct relation to the development of the fibrillar complex and the formation of the cell plate.

I have found (*FIG. 4*) as Strasburger did (*17, plate 7, figs. 30, 31*) that the daughter nuclei may remain at one side of the cell, close to the finished cell plate, while a portion of the phragmoplast develops progressively across the rest of the cell, thus reaching a position at a considerable distance away from the nuclei. This does not mean that the nuclei are not directly concerned with the further growth of the cell plate. In such cells the nuclei seem always to maintain a position equidistant from all parts of the greatly extended arc of kinoplasm. According to the figures I have observed in my sections, the size of the cell, in such cases is usually greater than in the cases in which the daughter nuclei migrate with the development of the cell plate and in which hence, the kinoplasmic ring usually has a smaller radius.

However, as I have stated before, the generally symmetrical position of the two nuclei with reference to the cell plate, and the fact that the cytoplasmic reticulum has at this time developed outward from the region of the daughter nuclei across the cell and along with the newly forming cell plate, provides that the fibrillar complex is still in definite cytoplasmic continuity with the nuclei.

Instances of the great distance to which the developing portions of the phragmoplast may go through the length of a very elongated narrow cell, are to be found in young sieve tubes, companion cells, procambium cells and other elongated vascular elements, in my sections through young petioles and the midribs of tobacco leaves. The figures confirm those of Bailey in all respects.

The movement of the daughter nuclei toward the cell plate and each other, bringing with them the cytoplasmic reticulum, is a conspicuous fact whose significance is not at all clear. This arrangement may simply provide for passing the "energizing" influence of the nuclei along the cytoplasmic strands to the region of fibril formation and growth about the periphery of the plate.

The most important typical figure of all the interrelations between daughter nuclei, general cytoplasm, fibrillar complex, and forming cell plate is probably to be found in such dense protoplasm as is found in pollen mother cells, root tip cells, etc. Timberlake's (22) *figs. 6, 7, and 8* of larch pollen mother cells, may be taken as such type figures. The whole cell division process involves a somewhat biconvex lens shaped region in which the daughter nuclei lie at the centers of the two faces of the lens and within its surfaces. The periphery of the lens is rounded and the curves of the elements of the fibrillar complex if continued would follow the surface of the lens figure and thus converge on a point occupying a position in the equator of the daughter nucleus. The longer fibers are on the periphery, and they shorten and fade out imperceptibly with the substance of the cell plate.

A conspicuous feature of this lens figure is that, with the exception of the elements mentioned—daughter nuclei and fibrillar complex, it appears quite devoid of stainable material. The cell plate appears as a thin line bisecting the whole figure. It is this absence of stainable material on both surfaces of the cell plate which suggests so positively that its material has been derived from the fibers which once filled this space.

The important rôle of the nucleus to various cell activities has been pointed out in many connections. In *Tradescantia* stamen hair cells, the circulating cytoplasmic threads are continually changing their position, swinging across the cell lumen through the cell sap, fusing with one another, etc. However, the prevailing direction of the streaming, as first described and figured in 1838 by Meyen (11), is to and from the nucleus.

Haberlandt's (5) description of the position of the nucleus in the developing root hairs is a familiar case. Here the nucleus lies right in the region of the first outward bulging of the epidermal cell wall, and moves out with the dense cytoplasmic material as the root hair grows in length.

Harper (6) concludes that the nucleus is the center of the activities concerned in forming the kinoplasmic fibers that bound the spore in free cell formation in the ascus, the special locus from which the fibrils develop being the central body on the surface of the nuclear membrane. That the nucleus is directly concerned in this formation of kinoplasmic material and the process of cell formation, is suggested by the fact that it is drawn out in the form of a long beak at whose tip is the active astral system. The ultimate fusion of the fibers side by side as their material flows down about the nucleus, results in the formation of an enclosing cell membrane.

Strasburger (19) holds that in cells with vacuoles, the laterally adjacent cytoplasm is soon drawn out into a thin sheath which surrounds the two daughter nuclei and encloses the fibrillar complex. Such a connecting sheath is not found in pollen mother cells of larch which are densely filled with cytoplasm, where however, the relation of the inner boundary of the surrounding cytoplasm with the fibrillar complex is the same. His *figs. 17 and 18, plate 2* (19) illustrate the shortening of the fibers of the central spindle to form the cell plate. *Fig. 19* shows the drawing back of the peripheral primary fibers from the cell plate already formed, thus drawing out the surrounding cytoplasm into a sheath around the spindle and the daughter nuclei. *Fig. 20* shows the same stage in a polar view. In *fig. 21*, the cell plate has reached one wall, while still continuing its movement across the mother cell on the opposite side. Here the cytoplasmic connection of the growing fibrillar complex and the daughter nuclei is clearly demonstrated. In *fig. 22*, the daughter nuclei in the completed daughter cells are shown once more suspended on radiating strands of cytoplasm.

The old question was whether new threads arise from the splitting of the old threads or *de novo*. If the threads are paths of flowage one could hardly admit of their splitting to form new threads. Such ideas as the threads giving rise by a splitting to new threads, or by a transfer of some of their substance into shorter threads first appearing between the longer threads, seem scarcely possible. The most satisfactory and reasonable explanation of their origin, is that they arise *de novo* in the cytoplasm about the periphery of the cell plate where they are being used up in its formation and growth.

The well known cytoplasmic aggregation around the nucleus that I have described as present in the early prophase, and often evident all through the stages of division, including the formation of the cell plate, is the notable feature in cell organization during the division stages. This is especially the case in highly vacuolated cells. Strasburger (19) describes this condition very clearly. It suggests without doubt that a relatively compact unit area, including both nuclei and cytoplasm, must be developed antecedent to the metabolic changes which lead to the formation of the kinoplasmic fibers in the polar caps, and later in the widening of the central spindle and the growth of the cell plate.

The rôle of the nucleus and later the daughter nuclei in these processes is by no means clear but it is fair perhaps to assume, that here, as in the other familiar cases noted above, it is in some way the centre of the metabolic changes which are taking place.

The relation of this cytoplasmic mass to the formation of the fiber groups and hence to the formation of the cell plate has not as yet been at all adequately cleared up, but the rearrangements in preparation for division which take place in much vacuolated cells and especially those with a single large central vacuole suggest its great importance.

Timberlake's (22) conclusion that the fibers can only arise in connection with the nucleus is in harmony with the facts as seen in cells of onion root tips, and larch pollen mother cells, where the peripheral threads of the spindle seem scarcely to lose their direct communication with the daughter nuclei through the whole development of the cell plate. The biconvex lens shape (Timberlake figures in *plate 8, figs. 6, 7, 8*) assumed by the fiber system in its late stages, emphasizes this conception.

In such vacuolated cells as I have studied, and for Bailey's procambial cell division, the case as to the origin of the new fibers at the periphery of the widening cell plate is not so clear. Bailey's figures are remarkable illustrations of the great extent to which the fiber complex must move in building the cell plate. Bailey (1) states, "The threads or 'lines of flow' do not extend across the cell from one tangential membrane to the other, but lie free in the cytoplasm. Nor are they connected with the daughter nuclei which remain in their original position near the center of the protoplast." "There is an enormous increase in

the number of 'peripheral' fibers during cytokinesis." "The phenomena appear to justify Strasburger's contention that the accessory fibers are of cytoplasmic origin."

If the fibers mark lines of flow, however, it is not impossible that in all these cases the form of the individual fibers is important. The fibers in my figures always curve inward toward the daughter nuclei, not only after they have lost all connection with the nuclei, but even when the fibrillar complex has migrated to a considerable distance across the cell away from the nuclei in those cases where the daughter nuclei have not accompanied the growing phragmoplast.

In my opinion, Beer and Arber's description of a new type of cell division by means of a "phragmosphere," the formation of a cell within a cell, the binucleate condition of this enclosed cell, and the cutting off of a cell without a nucleus are all based on a misinterpretation of polar views of the ordinary stages of cell division in vacuolated cells.

As I have explained, the "phragmosphere" is simply a polar view of a stage in progressive cell plate formation. The nuclei are not both left in the same cell, but one lies above, the other below the cell plate which is being formed within the kinoplasmic ring. There will be no cutting off of a cell without a nucleus since the ring of fibers will move out to the peripheral wall and cut off completely a lower and upper cell, not a cell within a cell as Beer and Arber describe.

Bailey (3) in a note on "Phragmospheres and binucleate cells" suggests that these investigators are simply describing stages in the division of parenchymatous cells, and that they present no evidence for the resorption of the central spindle without the formation of a cell plate, or the transformation of the phragmoplast with the associated cytoplasm into a hollow sphere, which will increase in diameter and form a hollow shell or cell within a cell. He (1) has correctly referred their description of such stages as they show in *figs. 1* and *20* to his *fig. 56, plate 29*. He interprets the situation as showing the wide view of the moving sphere of kinoplasm which has moved out from its original position between the two daughter nuclei, in *fig. 55, plate 29*. In *fig. 56*, we have the polar view of a similar stage where the circle of kinoplasmic material is in view as it lies between the two nuclei. The nucleus shown in *fig. 56*, appears

to lie above the sphere. In *fig. 57*, the two nuclei are visible, though situated at different levels in the section. The kinoplasmic complex here has reached the side walls of the cell and completed the cell plate in this region. Above and below, it continues building the cell plate which really extends from one arc of kinoplasm to the other, and lies between the two nuclei. A comparative study of longitudinal and cross sections demonstrates that such a plate actually does exist and is present even though indiscernable in a polar view.

Hutchinson (8, 9) also describes certain peculiarities existing in cell plate formation in the male gametophytes of *Abies* and *Picea*. The peculiarities referred to are in connection with the division of the primary cell to form a generative cell and tube nucleus. He claims that although thickenings of the fibers do occur in late telophase, yet no well defined cell plate is formed, but as the spindle begins to grow wider, it moves away from the tube nucleus, finally enclosing the generative nucleus only in a globe of fibers, as in his *figs. 11* and *12* (1914). The fibers finally touch the prothallial cell. Then they fuse side by side to form a hollow wall enclosing the generative nucleus alone. This wall formation is likened to that described by Harper in free cell formation of the ascospores in mildews.

It seems to me that Hutchinson's figures as drawn are not entirely consistent with his own interpretation. A careful study of his own figures, taking into account the planes of the sections from which they were taken, seems to me to show that the cell division has really taken place in the regular manner by means of cell plate formation within an enlarging kinoplasmic fibrillar ring. The phragmoplast in these pollen divisions instead of extending outward in the same plane to form a flat circular plate between the two daughter nuclei, which would eventually reach the peripheral walls as is usual, in this case curves around the generative nucleus, toward the prothallial cell, and in doing so lays down a cup shaped cell plate. This is very clearly shown in his *fig. 44* (1915). Here the cell plate may be distinguished in vertical section as a faint line extending between the two daughter nuclei, curving down around the generative nucleus, and terminating in the kinoplasmic fibrillar mass. With the further movement of the kinoplasmic material toward the prothallial cell, the cell plate is extended until it meets the prothallial cell

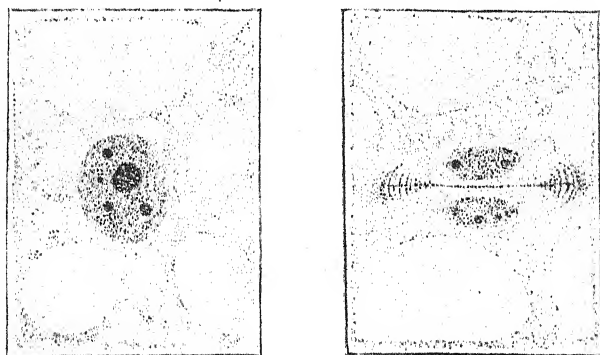
wall, thus cutting off by means of a cup shaped plate the generative nucleus from the tube nucleus. *Figs. 6, and 7, plate 15,* show the kinoplasmic fibrillar ring at the stage when the peripheral fibers no longer are attached to the daughter nuclei, but are arising anew in the cytoplasm as the cell plate widens. Contrary to Hutchinson's statement that the cell plate is not formed in the usual manner, but only when the fibrillar mass has moved away from the tube nucleus and surrounded the generative nucleus alone, in my opinion both these figures show conclusively that the cell plate has already been laid down in the usual manner, at the usual time. In these sections, the cell plate appears simply as a very plainly discernable line (edge view) apparent through the kinoplasmic fibrillar ring whose fibers curve distinctly inward about its periphery, toward the nuclei.

The figures so far discussed it seems to me admit of the interpretation I have suggested. *Fig. 8, plate 15,* however, seems really inconsistent with any hitherto known method of cell division. *Figs. 4, 18, 19, and 43* all show evidence of the thickening of the primary central spindle fibers which initiate the formation of the cell plate. *Figs. 23 and 45* show as distinctly as does *fig. 44,* previously explained, the kinoplasmic fibers still in process of formation to complete a cup shaped plate, which is evident in all these figures as a curved line (edge view) surrounding the generative nucleus.

Lawson's (10) description of a peculiar method of cell membrane formation in the multinucleate peripheral primary cells and central cytoplasmic region of the prothallium of *Cryptomeria japonica*, is referred to by Beer and Arber (4) as an example of the probable occurrence of phragmospheres such as they describe. Lawson states that cell plate formation here is by means of the lateral fusion of the fibers of a hollow spindle. However, it is quite clear, although all the stages in cell plate formation are not given, that the same misinterpretation is being made here as in Hutchinson's description of free cell formation in the pollen grains, by the fusion of fibers side by side to form an enclosing membrane. His *figs. 24, 31, and 32* suggest very strongly not the formation of a hollow sphere of fibers (the phragmosphere of Beer and Arber) but simply the presence of the usual ring of kinoplasmic fibers laying down the cell plate which will eventually separate the daughter nuclei. The

sections having been cut directly across the fibrillar ring and parallel to the cell plate, here present the fibrillar complex as a ring of granules, each granule being a cross section of a fiber.

Similar to this no doubt should be the explanation of Piech's (13) claim that free cell formation occurs in development of the cell boundary about the generative nucleus in the pollen grains of *Scirpus paluster*. He describes the formation of a free cell in the cytoplasm by the simultaneous formation of two enclosing membranes between the primary nucleus and the surrounding cytoplasm. Immediately after the formation of the two membranes a vacuolar region arises separating the two from each



FIGS. 1, 2. Cell division in cells somewhat older and larger than embryonic cells, with several vacuoles (Type 2).

other as shown in his *figs.* 31 and 32. Piech evidently has not found the stages of cell plate formation figured by Hutchinson (9).

Whether Strasburger's (16) well known figures of free cell formation in *Ephedra* are also to be interpreted as polar and oblique views of division by a cup shaped cell plate is in my opinion a possibility to be considered, though cup shaped cell plates are not known in connection with any other division in the embryo sacs. Certainly the embryo sac of *Ephedra* should be further studied.

Treub (23) recognized two types of cell plate formation, Strasburger (17) a third type, and Schürhoff (15) four so-called types of cell plate formation. Bailey (1) points out that the



differences in these various types are due merely to differences in the distribution of the elements of the cytoplasm in different tissue cells and the relative position from which the division figure is studied.

In my opinion it is worth while in the interest of clearness to recognize at least five distinct variants or conditions of cell content relations to cell plate formation. I am illustrating the essential stages in these variants by a series of text figures.

1. Cell division in small cells with relatively dense cytoplasm and no large vacuoles. This is the familiar case illustrated in the embryonic tissues of root tips, in pollen cells, etc. The growth of the cell plate in such cases involves only a simple widening out of the central spindle with the addition of relatively few new fibers to form ultimately a biconvex lens shaped phragmoplast. This would correspond to Schürhoff's first type. It is shown in many original drawings and text book illustrations. (Hof, *pl.* 3, 4.) (Timberlake, *pl.* 8.) I have not regarded it as necessary to give diagrams here.

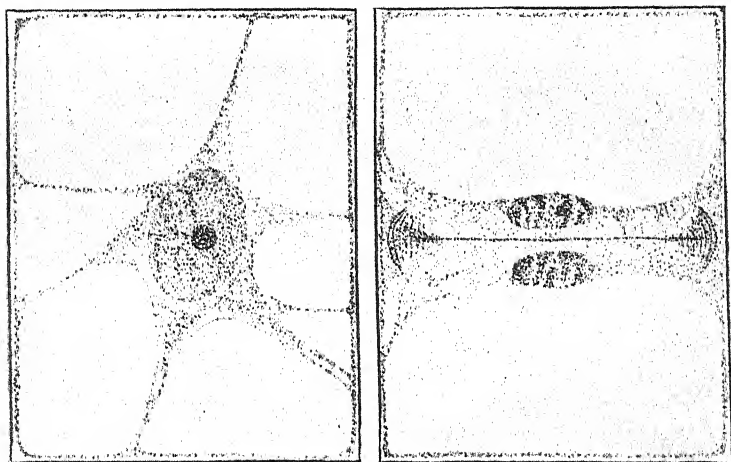
2. Cell division in somewhat larger cells containing several vacuoles. The nucleus lies in a dense mass of cytoplasm that occupies the central region of the cell. TEXT FIGS. 1 and 2 illustrate this type of cell, from a cross section of a very young leaf primordium below the growing tip of a tobacco stem. Such a division process differs in no essential features from that in embryonic cells.

3. Cell division in mature parenchymatous cells with a single central vacuole. Through this central vacuole extend cytoplasmic strands across the cell lumen connecting various regions of the primordial utricle. These tend frequently to be more or less centered on the nucleus and the streaming in them is sometimes said to be to and from the nucleus. Two cases of cell plate formation may be distinguished.

a. The nuclear division figure lies in the center of the cell, so that cell plate formation will go on progressively outward to the lateral walls of the cell, while the two daughter nuclei remain close to the cell plate in the original position occupied by the karyokinetic figure. TEXT FIGS. 3 and 4 are cells from the meristem of a tobacco plant stem growing tip, that illustrate this type. In polar view, the ring of kinoplasmic fibers would be visible about the two centrally placed nuclei, which typically

should appear to overlap. Such a ring of kinoplasm as it moves toward the periphery, and meets the walls of a many sided cell, may be divided up into one or more separate fibrillar arcs.

b. The nuclear division figure is eccentrically placed in the primordial utricle on one side of the cell, so that in cell plate formation one portion of the phragmoplast reaches the adjacent proximal lateral wall very soon, while the remaining arc of the fibrillar complex must develop peripherally across the entire cell to complete the cell division. If this arc should intercept the lateral walls at different times, it may as in (a), be broken



FIGS. 3, 4. Cell division in larger, more mature cells, containing a single large vacuole (Type 3a).

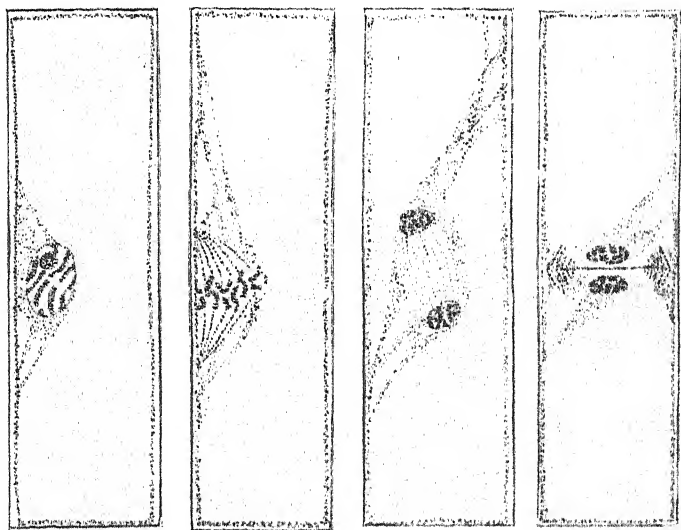
up into two or more separate arcs. The nuclei are usually located at a point equidistant from all parts of the kinoplasmic arc whether it is still entire or has been divided up into separate arcs by interception and fusion with the boundaries of the mother cell. If the kinoplasmic arc has a relatively small radius, the nuclei may accompany the fibrillar complex across the cell as Treub describes for his second type.

I include in this third group of division figures in large polygonal cells, several of the earlier recognized types. TEXT FIGS. 3 and 4, illustrate Treub's first type. PLATE 6 FIG. 4, illustrates Strasburger's third type. PLATE 6 FIG. 7, illustrates Schürhoff's

fourth type. PLATE 6 FIG. 10, illustrates Bailey's fifth type, as described for elongated cambial initials where the ring of kinoplasmic fibers is broken up into separate arcs.

4. Cell division in elongated cells containing a large central vacuole with practically no transverse cytoplasmic strands. During the resting condition, the nucleus lies in the primordial utricle. Cell division may take place longitudinally or transversely.

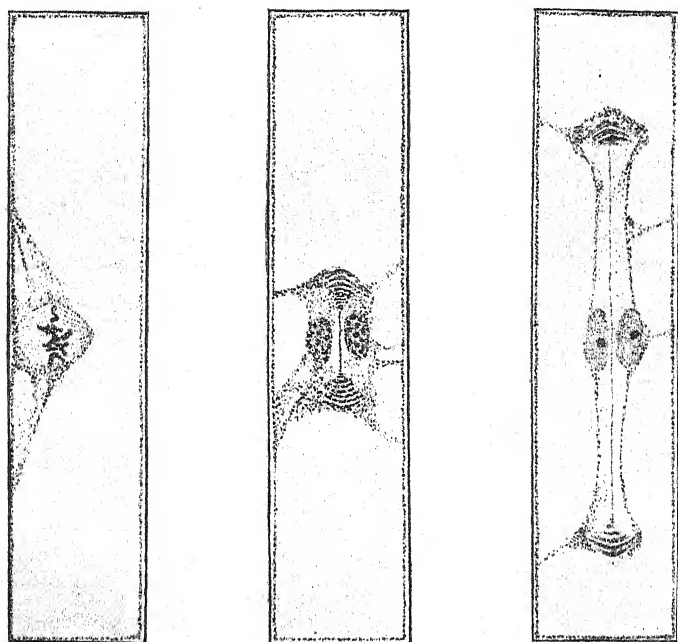
a. Transverse cell division in an elongated cell with one vacuole. The cytoplasm accumulates in the region of the nucleus



FIGS. 5-8. Stages in transverse division in an elongated vacuolate cell (Type 4a).

as it is about to divide so that the nucleus now lies somewhat away from the wall in the cell lumen, with cytoplasmic strands extending to the wall above and below it. The strands toward one end only move along the wall to the end of the cell, and cross it to the opposite lateral wall, so that the spindle figure now lies suspended in a diagonal massive strand or bridge of cytoplasm. Cell division now proceeds in the usual manner across the cell. TEXT FIGS. 5-8 illustrate the essential stages of such a division.

b. Longitudinal cell division in elongated cells with one large vacuole. TEXT FIGS. 9-11 show division stages in elongated vacuolated cells of the midrib of a very young tobacco leaf. The nucleus lies in the primordial utricle. The spindle and chromosomes are oriented for a longitudinal division even before the cytoplasmic strands in the manner described in 4a above, have drawn it away from the parietal layer and out into the



FIGS. 9-11. Stages in longitudinal divisions in an elongated vacuolate cell (Type 4b).

cell lumen. The cell plate is extended through the very long cell by two separate arcs of kinoplasmic fibers as in the elongated cambium initials described by Bailey. The entire fibrillar complex—cell plate, and peripheral kinoplasmic fibrillar arcs, is connected with the primordial utricle by strands of cytoplasm.

5. Cell division in such elongated elements as the cambial initials studied by Bailey, in which longitudinal division of the cell takes place by means of a very extended growth of the cell

plate through the great length of the cell. These are the most extreme cases of division by a cell plate so far observed, and their discovery by Bailey has brought the problems of cell division into a new light. As stated before, Timberlake's suggestion that the new fibers arise from the daughter nuclei seems hardly applicable here. None the less, as Bailey's figures show, the symmetrical position of the daughter nuclei with reference to the whole figure is a striking fact to be taken into account in any theory of the formation of the new fibers. As noted, I have observed such cell division figures only in petioles and midribs of very young leaves. The relative dimensions of the cells in the tissues I have studied are not so extreme as in the case of the cambium initials studied by Bailey.

It is obvious in all these cases that cell division by means of a cell plate is essentially the same process no matter how varied the distribution of the cytoplasmic and vacuolar content of the cell may be. In all we have a peripheral development of the cell plate formed from the original fibers of the central spindle.

The movement of the daughter nuclei toward each other and the forming plate, and the central position maintained by them with reference to the whole development of the fibrillar complex at the boundaries of the plate is very striking indeed. It is not until cell division is completed, and the cell plate has split to form two cell membranes, and a young cell wall has been laid down between them, that the daughter nuclei may migrate away from the forming wall.

Strasburger's conception of the fibers as threads of flow, which shorten, thicken, and fuse side by side to form the cell plate is perhaps as much in harmony with the facts as any of the various theories as to the fundamental nature of the processes here involved.

I gratefully acknowledge my indebtedness to Professor R. A. Harper for his many valuable suggestions in this study and in the preparation of this paper.

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## Explanation of plate 6

The drawings were made with the aid of the Abbe camera lucida. A Zeiss microscope was used with a 1 12 inch oil immersion objective and a number 3 ocular. These figures were drawn above stage level at a magnification of 1000 diameters, reduced in reproduction to about 666 diameters.

FIG. 1. Lateral view of a division figure in a cell from the growing tip of a healthy tobacco plant. The biconvex lens shape stage of the spindle has been reached. The young cell plate within the last fibers of the central spindle which form the biconvex lens, appears in edge view as a thin dark line.

FIG. 2. A lateral view of a cell plate formation figure in a cell from a transverse section of a growing tip of a diseased tobacco plant. The fibrillar complex on one side has reached the wall of the mother cell and is partially fused with it. Several plastids lie in the cytoplasm along the cell plate, here appearing in edge view as a line. The daughter nuclei already lie close to the cell plate.

FIG. 3. A lateral view of cell plate formation in a cell from a longitudinal section of a leaf primordium of a healthy tobacco plant.

FIG. 4. Lateral view of a late stage in cell plate formation in a cell from a healthy leaf primordium. Here the nuclei have remained on one side of the cell, while the fibrillar complex has travelled a considerable distance across the cell.

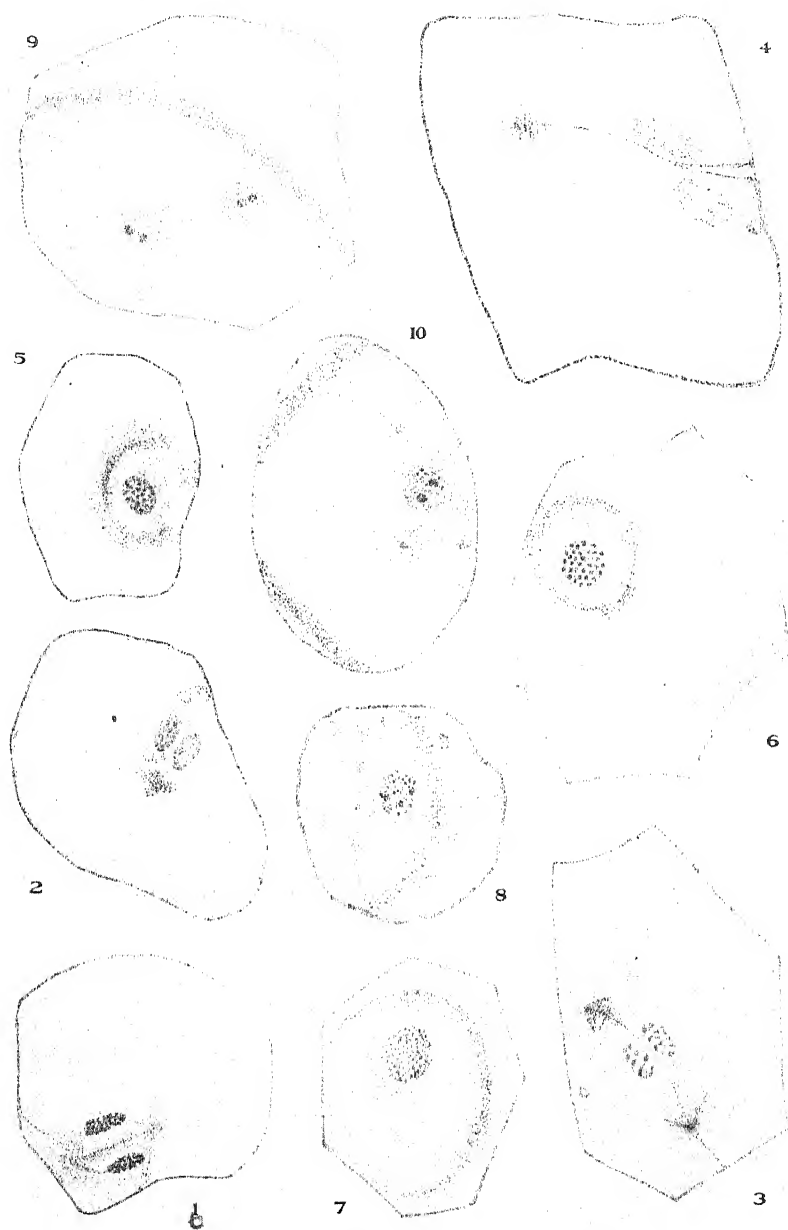
FIG. 5. A polar view of cell plate formation in a cell from a cross section of a healthy growing tip. The fibrillar kinoplasmic ring is almost entire. The cell plate which separates the two daughter nuclei within the ring, appears only as a faint granular haze. Several plastids lie in the cytoplasm about and within the ring.

FIG. 6. A polar view of a stage in cell plate formation from a cross section of a growing tip of a diseased plant. The cell is very large, and the section has not cut it favorably for showing the cytoplasmic strands about the fibrillar ring. One nucleus has been cut away, and the cell plate within the kinoplasmic ring is very clear as a round granular area which when seen in edge view on one side, appears as a thin line.

FIG. 7. Another polar view from the same section as in FIG. 6. This shows a later stage in cell plate formation. The fibrillar ring although nearly across the mother cell, has only merged with it in one corner of the cell. The two nuclei appear to overlap but lie one above the other with the delicate scarcely discernable cell plate between them. The cytoplasmic strands that lie along the surface of the cell plate are evident in this view.

FIG. 8. A somewhat tangential view of a late stage in cell plate formation in a cell of the growing tip of an old diseased plant cut in cross section. The fibrillar complex has intercepted the walls of the mother cell and now remains only as an arc of fibrillar material still moving across the cell. The cell plate which separates the two daughter nuclei is evident as a granular layer above which cytoplasmic strands and plastids lie. The lighter nucleus lies below the cell plate.

FIG. 9. A similar stage of cell plate formation to that shown in FIG. 8, in a very large centrally located meristematic cell in a cross section of a



GOLDSTEIN: CELL PLATE FORMATION





healthy growing tip. The cell plate, which lies above the more lightly stained nucleus and extends from one wall of the mother cell to the concave side of the fibrillar complex at its periphery, is scarcely evident. This arc of kinoplasm when viewed in a longitudinal section would appear as a fibrillar mass at the free end of the cell plate as shown in FIG. 4.

FIG. 10. A cell from the cross section of the growing tip of a diseased plant. Here the fibrillar complex has intercepted the wall in such a way as to leave two separate kinoplastic arcs. A portion of the cell plate which separates the two nuclei and which lies parallel to the section, is very clear on one side only as a very dark granular area. Where it sloped away from the plane of the section and therefore was not included in the section, it is only evident along the ring as a faint granular haze. The cell contains many plastids.



## Miscellaneous notes on plants of Southern California—IV\*

PHILIP A. MUNZ† AND IVAN M. JOHNSTON‡

In this paper the following abbreviations are used in citing herbaria: G, Gray Herbarium; NY, New York Botanical Garden; P, Pomona College; S, Stanford University; UC, University of California; and US, U. S. National Herbarium.

**Scirpus bernardinus** sp. nov. Perennial, forming a very dense turf commonly several meters in diameter; plants densely caespitose, crowded, commonly with hard short stout vertical caudices (these covered with the dark persistent stem-bases) terminating dark-colored rootstocks ca. 1 mm. thick, producing no underground resting buds; stems several, gray-green, leafless, obscurely 3-angled, striate, wiry, 3-10 cm. long, characteristically spreading and recurving, more or less interlacing with those of adjacent plants; sheaths obliquely truncate, pale brown, 1-2.5 cm. long; spikelets solitary, terminal, not subtended by an involucre bract, ovate-oblong, laterally compressed, 3-6 mm. long, ca. 2 mm. thick, 4-6-flowered; scales reddish brown, margins hyaline, midrib thickened and dark, apex obtuse; lowest scale deltoid-ovate, ca. 3 mm. long and broad, hyaline margin broad; upper scales oblong, 4-5 mm. long, ca. 2 mm. wide; styles 3-cleft, ca. 6 mm. long, branches 2.5 mm. long; stamens 3; filaments ca. 1 mm. long; anthers basifixed, erect, ca. 1 mm. long; bristles 3 (or more?), filiform, retrorsely barbed, equalling or surpassing the achene; achene oblong-obovate, coarsely beaked, ca. 1.8 mm. long, lenticular or obtusely trigonous, light brown, very lightly etched with longitudinal rows of more or less rectangular cells.

SAN BERNARDINO COUNTY: locally common in a wet meadow, South Fork of Santa Ana River, 8500 ft. alt., *Munz 6187* (TYPE, Pomona College Herb. no. 14332); South Fork of Santa Ana River, 8200 ft. alt., *Hall 7608* (G, UC).

Evidently a close relative of *S. pauciflorus* Lightf., under which species it has been placed by writers on the Southern Californian sedges. However, after a study of copious material of *S. pauciflorus*, from both North America and Europe, we have become convinced of the distinctness of the plant described

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\* The third paper of this series was published in the Bulletin for July, 1924 (51: 295-302).

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‡ Gray Herbarium, Harvard University.

above. It differs from its relative in its spreading recurved stems, densely caespitose turf-forming habit, and smaller, smoother, and less sharply angled achenes. The habit of growth is very peculiar, the plants forming a dense pure turf with the caudices so close and the stems so matted that a pick or collecting tool is driven into the mass with difficulty. It grows in the wet mountain meadows in the Canadian Zone of the San Bernardino Mountains where the frequent colonies are conspicuous because of their gray-green color, low dense growth and sharply defined limits. True *S. pauciflorus* is a very slender, erect, scarcely tufted plant with underground resting buds and very slender running rootstocks. In Southern California plants apparently referable to this species have been collected in the San Bernardino and San Jacinto mountains.

***Alnus rhombifolia* var. *bernardina* var. nov.** Leaves averaging smaller than in the typical form, 3-5 cm. long, 1.5-3 cm. wide, densely soft pubescent, not resinous, frequently noticeably double-serrate; staminate aments short, 2-4 cm. long, 3-4 mm. thick; pistillate aments smaller, less woody and more slenderly pedunculate, 7-12 mm. long, 5-7 mm. thick.

SAN BERNARDINO COUNTY: Santa Ana River at junction of South Fork, 6300 ft. alt., *Munz & Johnston* 8468 (TYPE, Pomona College Herb. no. 46794); South Fork of Santa Ana River, 6200 ft. alt., *Grinnell* 303 (UC); Lost Creek, 7000 ft. alt., *Munz & Johnston* 8615 (P); Foxessee Creek, 5500 ft. alt., *Munz & Johnston* 8669 (P); Hathaway Creek, 6000 ft. alt., *Munz & Johnston* 8671 (P).

A well marked but apparently local variation occurring in the pine belt of the San Bernardino Mountains in the upper portions of the Santa Ana River system between the altitudes of 5000 and 7000 ft. altitude. The most conspicuous character of the variety is the heavy pubescence on its leaves. At the lower edge of its range the variety grades off into the essentially glabrous and coarser plant of lower altitudes. It may eventually be found wise to include under the var. *bernardina* certain forms of *Alnus* from the pine belt of the San Jacinto Mountains and other ranges of Southern California, but at present these are excluded, for although approaching the variety *bernardina* in pubescence, they do not have small leaves and aments.

In the present connection it may be mentioned that the

reports of the occurrence of *A. tenuifolia* Nutt. in Southern California and Lower California seem erroneous. These reports are apparently based upon Sargent's statement of range in the *Silva* of North America (9: 76. 1896). According to Sargent the species forms "great shrubby thickets six or seven thousand feet above the sea along the head-waters of the rivers of southern California which flow to the Pacific Ocean." Such collectors as Parish, Hall and Abrams have never reported thickets of any alder in the higher mountains of Southern California and have never recorded any specific occurrence of *A. tenuifolia* there. More recent collecting on our part in almost every portion of the region has likewise resulted negatively in this regard. Furthermore, search in all the important herbaria of the country including that of the Arnold Arboretum, has failed to yield any material of *A. tenuifolia* from south of the main Sierra Nevada of central California (Kern County?). Similarly no specimens have been found from Lower California. Examination of the cited reference, i. e. *Zoe* 4: 216. 1893, upon which Sargent, l. c., apparently based the inclusion of Lower California within the range of *A. tenuifolia*, shows that it was misread. The citation given refers to an *Alnus* reported by Katherine Brandegee from Bouldin Island in the lower San Joaquin Valley of California which was probably assumed to be from Lower California inasmuch as the preceding article in the journal was by T. S. Brandegee and concerning the flora of northern Lower California. In Mr. Brandegee's article no *Alnus* was mentioned.

Because of their well developed double serration the leaves of *A. rhombifolia* var. *bernardina* suggest those of *A. tenuifolia* rather than those of typical *A. rhombifolia*. The staminate aments of the variety, however, are clearly those of *A. rhombifolia*.

***Malvastrum gabrielense* sp. nov.** An erectly branched shrub ca. 2 m. high; branches rather slender, virgate, with a dense close stellate-pubescence; leaves scattered, firm, shorter than the internodes, 2-4 cm. long, 1.5-2.5 cm. broad, obscurely 5-lobed, coarsely and irregularly serrate-dentate, stellate-pubescent, pale green, beneath somewhat lighter and prominently veined, apex broadly acute, base somewhat cordate; petiole densely stellate, 5-15 mm. long; stipules subulate, 8-9 mm. long, early deciduous; flowers in few-flowered glomerules in the upper axils; pedicels 0-3 mm. long; bractlets subulate, 7-12 mm. long, shorter

or longer than the calyx; calyx 10-12 mm. high, loosely stellate-pubescent, simply tomentose inside; calyx-lobes lance-ovate, ca. 8 mm. long, 3 mm. broad, strongly acuminate, enervous; petals pink, 16-18 mm. long, 8-9 mm. wide, strongly oblique-asymmetrical, sessile, rounded above; styles ca. 8 mm. long; style-lobes glabrous, slightly thickened at summit, 2-3 mm. long, ca. 10; stamens ca. 50, glabrous except at very base; connective prolonged as a subulate appendage which about equals the length of the anther-sacs; ovary stellate-pubescent; mature fruit unknown.

LOS ANGELES COUNTY: Arraster, north slope of San Gabriel Mountains, 3100 ft. alt., *F. W. Peirson 774* (TYPE, Pomona College Herb. no. 9927).

*Malvastrum gabrielense* appears to lack obvious relationships. From *M. orbiculatum*, with which it grows, it differs in its small more angular, thinner, less pubescent leaves, less densely pubescent stems and calyces, and more elongate calyces, bractlets and stipules. Though more leafy above, the inflorescence of the new species suggests the interrupted glomerate one of *M. viscidum*, a more southern species with hispid calyces.

***Ammoselinum occidentale*** sp. nov. Annual scabridulous herb 10-15 cm. high, with numerous strict simple leafy branches; stems slightly angled, reddish tinged; leaves glabrous, ternately divided, 25-45 mm. long, ultimate segments linear, 5-8 mm. long, ca. 1 mm. wide; petiole of lower leaves becoming 25 mm. long, with an evident subsheathing hyaline-margin, that of the slightly reduced upper leaves much shorter; umbels compound, on naked terminal peduncles 15-50 mm. long that slightly surpass the leaves; involucre absent; involucels linear-lanceolate, few, 3-5 mm. long, ciliate-denticulate; rays unequal, ascending, several, 2-8 mm. long; pedicels very unequal, 1-4 mm. long, angled; petals white, broadly obovate, ca. 0.8 mm. long, obtuse; sepals undeveloped; fruit (submature) ovate-oblong, ca. 3 mm. long; stylopodium conical; carpels obscurely 5-angled, closely armed with unequal stout subulate hairs; oil-tubes in triplicate under the 4 dorsal and lateral furrows, those of the commissural face larger, more separated and 4 in number; seed compressed dorsally, face plane.

RIVERSIDE COUNTY: locally abundant in heavy soil of a dry basin under shrubs and in the open, "Hayfields," Chuckwalla Valley, Colorado Desert, 500 ft. alt., April 13, 1922, *Munz & Keck 4930* (TYPE, Pomona College Herb. no. 13255).

This species is a very evident relative of *A. giganteum* C. & R. of Arizona and Coahuila, from which it differs in its lower,

more compact habit, unbranched stems, smaller more compact umbels, pubescent (rather than conspicuously callous-toothed) smaller carpels, and twice as numerous commissural oil-tubes. Like its relative, the proposed species differs from the two other members of the genus, i. e. *A. Popei* T. & G. and *A. Butleri* (Engelm.) C. & R., in having the lateral and dorsal oil-tubes in threes rather than solitary. For the two western species which have triplicate oil-tubes we are proposing the section **Hesperoselinum**. The relationship and the characters of the 4 species now referred to the genus *Ammoselinum* may be appreciated by a study of the following natural key.

Dorsal and lateral oil-tubes solitary, one under each furrow; carpels smooth or inconspicuously roughened. §*Euammoselinum*.

Umbels sessile in the axils; commissural face of carpel not corky-thickened; fruit 2 mm. long or less, broadly ovate, smooth or nearly so.....*A. Butleri*.

Umbels terminal and evidently peduncled; commissural face of carpel with 2 strongly thickened corky ridges; fruit 3-4 mm. long, oblong-ovate, somewhat roughened.....*A. Popei*.

Dorsal and lateral oil-tubes in threes; carpel roughened or coarsely pubescent. §*Hesperoselinum*.

Fruit covered with coarse subulate hairs; commissural oil-tubes 4; stems simple, 1-1.5 dm. tall.....*A. occidentale*.

Fruit covered with blunt callous teeth; commissural oil-tubes 2; stems loosely branched, 2-3 dm. tall.....*A. giganteum*.

**Penstemon Peirsoni** sp. nov. A pallid glabrous decumbent plant ca. 3 dm. tall; branches basal, erect, simple, ca. 3 mm. thick, internodes 2-4.5 cm. long; leaves rather firm, glaucescent, concolored, nerveless, inconspicuously dentate; basal leaves oblanceolate, obtuse, basally attenuate, 4-7 cm. long, 7-10 mm. broad, with petioles about 1 cm. long; middle cauline leaves gradually reduced, lanceolate, acute, subamplexicaul, 1-5 cm. long; inflorescence rigid, few-flowered, 8-13 cm. long, 2.5-4 cm. thick, narrowly and inconspicuously bracteate; peduncles 5-10 cm. long, curved upward and vertical above; pedicels slender, glabrous, 3-15 mm. long, usually strict, subtended by acute herbaceous lanceolate bracts 2-3 mm. long; calyx puberulent; calyx-lobes imbricate, acute, 4-5 mm. long, lateral margins white-hyaline; corolla about 2.5 cm. long, entirely glabrous, purplish-lavender; tube ca. 5 mm. long and ca. 3.5 mm. thick; throat ca. 15 mm. long, 7-8 mm. thick, weakly inflated; upper lip 4 mm. long, ca. 7 mm. broad, erect (?), lobes 2, ca. 1.5 mm. long, obtusely deltoid; lower lip 5 mm. long, ca. 9 mm. broad, erect, lobes 3, ca. 3 mm. long, ovate; sterile filament yellow-



bearded near tip, ca. 19 mm. long, reaching to corolla-sinuses; fertile stamens glabrous, reaching to corolla-sinuses; anther-sacs glabrous, ca. 1.7 mm. long, oblong-ovoid, ultimately explanate, lines of dehiscence confluent and extending to the base of each sac; mature fruit unknown.

VENTURA COUNTY: single plant on dry slope, Seymour Creek, Mt. Pinos, 5900 ft. alt., June 10, 1923, *Munz 6999* (TYPE, Pomona College Herb. no. 31596).

Apparently most related to *P. fruticiformis* var. *incertus*, but differing in its broader serrulate leaves, narrower stricter thyrse, and smaller, glabrous, less inflated and more colored corollas. In gross habit it much suggests *P. heterophyllus* but has broader glaucous denticulate leaves, broader and shorter sepals, smaller less inflated lavender corollas, bearded sterile filament and completely dehiscent divergent explanate unappendaged (not subulate ciliate) anther-sacs. In our recent paper (Bull. So. Calif. Acad. 23: 34. 1924) the type of *P. Peirsoni* is mentioned as a possible hybrid between *P. heterophyllus* and *P. Palmeri* var. *Grinnellii*. However, since recent critical restudy of the plant has shown that it does not have the anther-sacs of *P. heterophyllus* as once supposed, and particularly since *P. heterophyllus* is not known from the Mt. Pinos region, it now seems that the suggested parentage is improbable if not impossible. In its bearded style and elongate glaucous foliage *P. Peirsoni* is very suggestive of *P. fruticiformis* and its variety. Going southwest-ward towards Mt. Pinos from the type locality of *P. fruticiformis* the plants of this relationship are represented by the var. *incertus* which has less inflated, less bearded, more colored corollas. Hence the still less inflated, comparatively deeply colored glabrous flowers of *P. Peirsoni* seem the natural culmination of the trend which partially characterizes the var. *incertus*. *Penstemon Peirsoni* has leaves which are denticulate and broader than those of the var. *incertus*, being in these respects more like typical *P. fruticiformis*.

It is a pleasure to associate with this striking plant the name of Mr. Frank Peirson, of Pasadena, whose persistent collecting in the wilder portions of the deserts and mountains is adding much to our knowledge of the flora of our region. Mr. Peirson was with the senior author when the type of the new species was collected.

CHRYSOPTIS BREWERI A. Gray, Proc. Am. Acad. 6: 542.

1865. (*Chrysopsis Wrightii* A. Gray, Synop. Fl. N. Am. ed. 2. 1<sup>2</sup>: 446. 1886.)

An examination of the type of *C. Wrightii* and a comparison of it with the suite of 21 specimens which now represents *C. Breweri* in the Gray Herbarium, has proved the essential identity of these two species. The type and only known collection of *C. Wrightii* consists of two stems just coming into flower, only one head, in fact, having open florets. The material is quite similar in habit and technical characters to Sierran collections at the same stage of development.

*Chrysopsis Wrightii* was discovered by W. G. Wright in 1882 about the summit of San Gorgonio Peak, the highest summit of the San Bernardino Mountains, and has been vainly sought by botanists later visiting that area. The presence of this very rare and local species in the San Bernardino Mountains has been very puzzling since it has been the only one of the endemic species of the pine belt of that mountain-mass which has not been repeatedly recollected. On the other hand its apparent rarity is quite typical of an increasing list of boreal species of the Sierra Nevada that have a very local or rare occurrence in the San Bernardino Mountains. As a synonym of *C. Breweri* the distribution of *C. Wrightii* is quite analogous to that of such species as *Crepis nana* Rich., *Senecio occidentalis* (Gray) Greene, *Sibbaldia procumbens* L., *Salix orestera* Schneid., *Parnassia californica* Greene, etc., all of which are widely distributed in the Sierras of central California and known in Southern California only through single collections.

***Taraxacum californicum*** sp. nov. Plant 5-20 cm. high, usually glabrous; root rather thick, simple, dark, glabrous; leaves ascending to widely spreading, light green, oblanceolate, 5-10(-13) cm. long, usually 1-2 (or rarely nearly 3) cm. broad, obtuse or acutish, characteristically subentire or sinuate-dentate but occasionally somewhat runcinate-incised, long attenuate at base, in age promptly and cleanly disarticulating from the collar; scape one to several, suberect to decumbent, at anthesis more or less equalling the foliage but finally elongating, glabrous even when young; heads stout, broadly cylindrical, 10-15 mm. long, 8-12 mm. thick, very abruptly contracted at base and hence truncate; tegules numerous, strictly erect, practically ecorniculate, light green or less commonly dark, usually somewhat pruinose, commonly with a narrow scarious margin; exterior tegules not half the length of the inner ones, ovate-

lanceolate, acute, 5-7 mm. long, appressed; inner tegules linear-lanceolate, 12-15 mm. long, 2-3 mm. wide; flowers numerous, suberect, yellow, at anthesis surpassing tegules by 2-3 mm.; achenes pale brown, ca. 3 mm. long, coarsely rugose, above narrowly tuberculate and abruptly attenuate (not with a well developed snout); beak slender, 7-9 mm. long; pappus white, ca. 5 mm. long.

SAN BERNARDINO COUNTY: meadows east of Bluff Lake, *Munz* 5630 (P); Bear Valley, *W. M. Pierce* 101 (TYPE, Pomona College Herb. no. 12629); Bear Valley, *Parish Bros.* 1461 (G, S, US); Bear Valley, 6500 ft. alt., *Parish* 4977 (NY, S, US); Bear Valley, *Parish* 3131 (US); South Fork Meadows, Santa Ana River, 8200 ft. alt., *Hall* 7512 (UC); Mare Flats, *Crawford* 946 (P, UC); Cienega Seca Creek, *Munz* 6305 (P).

This species, the only native *Taraxacum* known from west of the Great Basin, is common in wet soil in the pine belt of the San Bernardino Mountains where it occurs from 6000 to 8500 ft. altitude. In Southern Californian references it has passed mainly as *T. officinale* var. *lividum* Koch, e. g. Hall, Univ. Calif. Pub. Bot. 3: 272. 1907. In the monograph of the genus by Handel-Mazzetti (Monog. 74. 1907) it was referred to *T. lapponicum* Kilim., and in Sherff's recent treatment of the North American species of *Taraxacum* (Bot. Gaz. 70: 342. 1920.) it was included in *T. ceratophorum* DC. From these species, however, *T. californicum* is readily separated, not only by its remarkably isolated range, but by having stocky cylindrical heads which are truncate at the base, small achenes, non-spreading scarcely exserted florets, and erect appressed ecoriuculate tegules.

## Notes on Fabaceae—V

PER AXEL RYDBERG

### XYLOPHACOS: III. MISSOURIENSES

This group is characterized by the straight pod, the two sutures being about equally curved, and the apex rather abruptly acute, not at all upturned; otherwise the plants are of the same habit as those of the preceding group.

Pod obcompressed, the upper suture only prominent;

hairs acute at each end..... 22. *X. vespertinus*

Pod compressed, both sutures prominent.

Corolla nearly 2 cm. long, purple; calyx-lobes

nearly half as long as the tube..... 23. *X. missouriensis*

Corolla about 15 mm. long, white or merely purple-tinged, with a purple keel; calyx-lobes about one

fourth as long as the tube..... 24. *X. cymboides*

22. XYLOPHACOS VESPERTINUS (Sheldon) Rydberg. Jones (*Astragalus* 215. 1923.) reduced this to a variety of *Astragalus amphioxys*, which it resembles a good deal in general habit and pubescence, but the pod is totally different and approaches that of *X. missouriensis*. I think that *A. chamaelucæ panguicensis* Jones is the same. Jones transferred the latter to a variety of *A. argophyllus*, then raised it to specific rank and lastly returned it back to a variety of *A. amphioxys*.

COLORADO: Grand Junction, *Eastwood*, in 1892; collector not given, in 1894; Evans, *Johnston* 635; Arboles, *Baker* 417; Naturita, *Payson* 309; Durango, *Eastwood* 5293.—NEW MEXICO: Colfax Co., 20142; Sacramento Mountains, *Earle* 551, *Aztec*, *Baker* 418; San Andreas Mountains, *Wooton*, in 1913; Pecos, *Standley* 5020; Socorro, *Eggleston* 16244; Otero County, *Eggleston* 14411; *Wooton*, in 1897; San Antonio, *Wooton* 3841; Raton, *Standley* 6266; Union Co., 6240; Farmington, 7097; Sandia Mountains, *Ellis* 434; Carriso Mountains, *Matthews* in 1892; Greenville, *Eggleston* 20096; Romaldo, 2011.

23. XYLOPHACOS MISSOURIENSIS (Nutt.) Rydberg. *Astragalus missouriensis* was described from material collected in Upper Louisiana, probably somewhere in South Dakota. It is characterized by the more or less black-hairy calyx and the

peculiar pod, which has both sutures prominent especially when ripe, when the pod splits along both sutures. It is common from Saskatchewan and Alberta to South Dakota, Oklahoma, and Colorado, east of the mountains. It has been reported from New Mexico and Texas, but I have seen no specimens. *Fendler 149, Edwards, and Earle 82* from Santa Fe (all in flowers only) seem to be *X. pephragmenus*; *Bro. Anct 103* seems to be *X. cyaneus*, and *Standley 5020* and *Baker 418, X. vespertinus*.

#### IV. PYGMAEI

This group resembles much the CYANEI, but the pericarp of the fruit is pulpy and in age becomes dry and spongioid, the exocarp at last becoming papery and separating from the endocarp.

Leaflets 7-11, obovate, obtuse.

Pod straight, elliptic in outline. . . . . 24. *X. cymboides*

Pod somewhat arcuate, lance-ovoid in outline. . . . . 25. *X. pygmaeus*

Leaflets 1-5, lanceolate, acute; pod arcuate. . . . . 26. *X. musiniensis*

24. XYLOPHACOS CYMBOIDES (M. E. Jones) Rydberg resembles closely *X. missouriensis* in habit, flowers, and fruit, but the flowers are smaller and paler and the fruit is less woody and the thinner exocarp separates in age from the endocarp somewhat as in *X. pygmaeus* and *X. musiniensis*.

*Astragalus amphioxys cymellus* M. E. Jones (*Astragalus* 215. 1923) is a synonym of this, at least as to a specimen in Jones' herbarium, marked "Part of Type," from San Raphael Swell, the type locality given in the original description. This specimen can not be distinguished from the other species cited below, all from the same county of Utah.

UTAH: Huntington, Jones 5464 j; Emory, 5445 f; Spring Glen, Jones, in 1896; San Raphael Swell, Jones, in 1914.

25. XYLOPHACOS PYGMAEUS (Nutt.) Rydberg. This species was first described as *Phaca pygmaea*. As there was already an *Astragalus pygmaeus*, Dr. Gray proposed the name *A. Chamaeluce* but placed it next to *A. tephrodes* and *A. aridus*. Sheldon followed Gray and added to the group *A. castanaeformis* and *A. Newberryi*. Jones redescribed it under the name *A. Cicadae*. After discovering that he had redescribed *Phaca pygmaea* or *Astragalus Chamaeluce*, he made his species a variety thereof

without pointing out any distinctive characters. In his Revision he adopted the name *Astragalus pygmaeus*, although at least two species had been described previously under that name.

COLORADO: De Begue, *Osterhout 4467*.—WYOMING: Fort Bridger, *A. Nelson 4605*; Green River, *Rydberg*, in 1895; Ham's Fork, *Nuttall*.—UTAH: Emery County, *Jones*.

26. XYLOPHACOS MUSINIENSIS (M. E. Jones) Rydberg. This resembles *X. medius* Rydb. in pubescence and in the form and pubescence of the leaflets, but the latter are seldom more than two pairs and the pod has the structure of that of *X. pygmaeus*. The type came from Ferron, Utah. Other specimens seen are from Spring Glen, Emery County, collected by Jones.

#### V. ERIOCARPI

This group combines the appressed silvery pubescence of the preceding group with the woolly pod of the next following:

Leaves elliptic or oblanceolate to obovate; calyx-teeth one-fourth to one-third as long as the tube.

Leaflets 5-7, broadly oblanceolate to obovate, silvery white, pod densely villous

Leaflets mostly obovate, obtusish; peduncles much shorter than the leaves. . . . . 27. *X. Newberryi*

Leaflets oblanceolate, mostly acute; peduncles about equalling the leaves. . . . . 28. *X. medius*

Leaflets 9-19, merely canescent, rarely more than 1 cm. long; pubescence of the pod comparatively sparse.

Leaflets 3-8 mm. long, elliptic to oval, obtuse. . . . . 29. *X. marianus*

Leaflets 8-15 mm. long, lance-elliptic, acute. . . . . 30. *X. eurekaensis*

Leaves broadly obovate-cuneate, rounded, truncate or retuse at the apex; calyx-teeth half as long as the tube. . . . . 31. *X. Watsonianus*

27. XYLOPHACOS NEWBERRYI (A. Gray) Rydberg. This was first collected by Newberry on the Ives Colorado Expedition, and really was the plant that Dr. Gray had in mind, when he changed *Phaca pygmaea* Nutt. to *Astragalus Chamaeluce* A. Gray. As Gray expressly stated that he was obliged to change the name *P. pygmaea*, the latter must be regarded as the type of *A. Chamaeluce*. *X. pygmaeus* and *X. Newberryi* are very much alike in habit, and, mainly differing in the fruit, it was not surprising that Gray regarded Newberry's plant,

collected in flower only, as the same as that of Nuttall. *A. candelarius exiguus* Sheldon as to the Utah specimens is nothing but *X. Newberryi*.

Jones' variety *A. Newberryi castoreus* differs little from the type, the calyx-lobes being slightly blackish. His hybrids *A. Purshii*  $\times$  *Newberryi* (as to the Nevada specimens named by Jones) and *A. Purshii Watsonianus* (*Astragalus* 216. 1923) belong also here, and do not differ from the var. *castoreus*. In his monograph, Jones does not cite any specimens of *A. Purshii*  $\times$  *Newberryi* from Nevada, but in his herbarium, now at Pomona College, there are three specimens so labelled, two from Auburn and one from Centerville, and one of *A. Purshii*  $\times$  *Watsonianus* also from Centerville of the same date. These are all the same but have nothing to do either with *X. Purshii* or *X. Watsonianus*.

WYOMING: Fort Bridger, *A. Nelson* 4605.—UTAH: Milford, Jones, in 1880; Stokes, in 1903; St. George, Jones 5006; Marysvale, 5338 l; Panguish, Palmer; Dugway, Jones, in 1891; Glenwood, Ward 225.—ARIZONA: NEWBERRY (Ives Expedition); Peach Springs, Jones, 68; Lemmon.—NEW MEXICO: Aztec, Baker 420.—CALIFORNIA: Inyo County, S. W. Austin 529.—NEVADA: Palmetto Range, Purpus 5868; Centreville, Jones, in 1893 (labeled *Astragalus Purshii*  $\times$  *Watsonianus*); Aurum and Centreville, Jones, in 1893 (labeled *A. Purshii*  $\times$  *Newberryi*); Austin, Hitchcock 767.

28. *Xylophacos medius* Rydberg, sp. nov. (*Astragalus eriocarpus* M. E. Jones, Zoe 3: 293. 1893. Not S. Wats. 1871. *Astragalus consectus* Sheldon, Minn. Bot. Stud. 1: 143, in part, 1894. *Astragalus Newberryi*  $\times$  *eurekensis* Jones, *Astragalus* 217. 1923.)

Subacaulescent perennial, with a caespitose leafy caudex; leaves 4-7 cm. long, ascending; stipules lanceolate, 3-5 mm. long; leaflets 5-9, oblanceolate or rhombic-oblanceolate, acute, 1-2.5 cm. long, 5-8 mm. wide, silky-canescens on both sides; peduncles 5-8 cm. long; racemes 3-6-flowered; bracts lanceolate, 5-6 mm. long; calyx strigose, somewhat nigrescent, the tube about 1 cm. long, the teeth 2-3 mm. long; corolla 2-2.5 cm. long, purple-tinged, the keel with a dark purple tip, otherwise as that of *X. Newberryi*; pod villous, the hairs becoming tawney in age, obliquely lance-ovoid in outline, 2 cm. long, rounded at the base, arcuate, 1 cm. broad and 5-7 mm. deep.

Type collected at Lake Point, Utah, May 29, 1880, Jones 1743 (herb. N. Y. Bot. Gard.).

This species was first collected in Southern Utah (Parry 44) and named *A. eriocarpus* S. Wats. Sheldon included this specimen in his *A. consectus*. It was then collected at Dog Valley, Utah (Jones 1690) and named *A. Chamaeluce*. This number as represented in the Torrey herbarium is in early bloom, and the leaves not fully developed. Jones later changed the name to *A. cibarius* Sheld., which name belongs to Jones' own *A. arietinus*. From what can be judged from a later statement of Jones, (Contr. W. Bot. 8: 12. 1898) it seems as if he intended to include this in his *A. eurekaensis*. Later in the year Jones collected apparently the same species at Lake Point (Jones 1743), which he named *A. eriocarpus* S. Wats. Sheldon determined this number as *A. suturalis* Sheld., which is merely a substitute of name. At last Jones (Astragalus 217. 1923) based on this number his *A. Newberryi*  $\times$  *eurekaensis*. There is no evidence given by Jones why this should be regarded as a hybrid. I have seen no specimens either of *X. Newberryi* or of *X. eurekaensis* from the Great Salt Lake valley. That the plant is somewhat intermediate between the two species is not proof enough that it is of hybrid origin. From *X. eurekaensis* it differs in the more brightly colored corolla, the less numerous, larger and comparatively broader leaflets; from *X. Newberryi* in the larger acute leaflets and the longer peduncles; and from *X. Watsonianus* by the fewer, narrower, acute (not rounded to retuse) leaflets, the shorter flower, the shorter calyx-lobes and shorter and less curved pod.

UTAH: Lake Point, Jones 1743; Dog Valley, 1690; southwestern Utah, Parry 44.

29. *Xylophacos marianus* Rydberg, sp. nov. Subacaulescent perennial, with a caespitose caudex; stems 1-3 dm. long; leaves 3-7 cm. long, with a slender rachis; stipules ovate or deltoid, 2-4 mm. long; leaflets 11-19, oval, obovate, or broadly elliptic, mostly obtuse, 3-8 mm. long, grayish-strigose; peduncles 2-4 cm. long; racemes 2-6-flowered; bracts lanceolate, 3 mm. long; calyx villous, the tube 8-10 mm. long, the teeth subulate, 3 mm. long; corolla about 2 cm., rarely 2.5 cm. long, apparently only purple-tinged; banner obovate, slightly arcuate; wings shorter, the blades oblong, with a broad auricle; keel-petals still shorter, the blade broadly lunate, rounded at the apex; pod lance-ovoid, 15-18 mm. long, 8 mm. broad and deep, moderately arcuate throughout, villous but not densely so.



Type collected at Marysvale, Utah, June 1, 1894, *Jones* 5355 (herb. N. Y. Bot. Gard.).

The type was distributed as *Astragalus Purshii*, but the plant is evidently more closely related to *X. eurekaensis*, from which it differs in the smaller, comparatively broader, obtuse leaflets, and the smaller less curved pod. Apparently the same plant, but stouter than the type, was collected in flower only near Utah Lake by Fremont and distributed as *Astragalus missouriensis*. Dr. Gray changed the determination to *A. Shortianus minor*, to which it is not closely related.

It is also *Astragalus Purshianus* × *Newberryi* Jones (*Astragalus* 216. 1923) mainly, but I do not think it is a hybrid of the two, having much smaller flowers than either. The only character in which it approaches *H. Newberryi* is the appressed pubescence, but at the same time this is shorter and coarser. The specimens from Dugway and Cedar Fort were included in Jones' so-called hybrid.

UTAH: Marysvale, *Jones* 5355; Cedar City *Jones* 5200; Fish Lake Cañon, *Garrett* 2513; Utah Lake, *Fremont* 406, in 1845; Dugway, *Jones*, in 1891; Cedar Fort, *Jones*, in 1896; Fish Lake Forest, *Eggleston* 11108, 11139, 11109; Ephraim, *Tidestrom* 532, 104; Homansville, *Jones* in 1891; Loa Pass, 5639 g; Soldier Summit 5601 c; Jugtown, 5405 c.

30. XYLOPHACOS EUREKENSIS (M. E. Jones) Rydberg. This species resembles *X. argophyllus* a good deal in habit and leaf-form, but the pod is different, being silky villous, though not as densely so as in *X. Newberryi* or *X. medius*. In this respect it resembles more that of *X. glareosus*, from which it is most easily distinguished by the appressed pubescence of the leaves.

For many years Jones regarded this as *A. glareosus*. Upon discovering his mistake he substituted the name *A. eurekaensis* Jones (*Contr. W. Bot.* 8: 12. 1898). He did not cite any specimens, however, and hence no type locality is given. We might assume that it is Eureka, Utah, where he collected specimens in 1891. The sheet of this collection in the Gray Herbarium represents a depauperate form, but specimens from Cedar Fort, in 1896, show the other extreme of the species.

UTAH: Eureka, *Jones*, in 1891; Cedar Fort, *Jones*, in 1896; Ephraim, *Tidestrom* 2083, 1000.

31. XYLOPHACOS WATSONIANUS (Kuntze) Rydberg. This differs from its nearest relatives in the broad leaflets, rounded to retuse at the apex, the larger flowers, darker calyx, longer calyx-teeth and longer pod, strongly arcuate towards the tip. It was originally described as *A. eriocarpus* S. Wats.; there being an older *A. eriocarpus*, the name was changed to *Tragacantha Watsoniana* Kuntze and *Astragalus suturalis* Sheldon. Jones reduced it to a variety of *A. Newberryi* using first *eriocarpus* then *Watsonianus* as varietal names. Jones included in it *A. candelarius* Sheldon, but I think erroneously. He stated (*Astragalus* 217. 1923) that it is "common throughout the Great Basin from the base of Wasatch to the Sierras and southward to Owen's Valley and the southern flanks of the Mogollons of Arizona." Even if *A. candelarius* is included, this area is altogether too large. I know it only from the type collection from Coyote Mountains, Nevada (apparently West Humboldt Mountains). Watson also recorded it from the Trinity and East Humboldt Mountains. Stokes' specimens from Palisades may belong here also.



# INDEX TO AMERICAN BOTANICAL LITERATURE

1911-1925

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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**Abbott, W. L.** Botanical exploration of the Dominican Republic. Smithsonian Misc. Coll. 74<sup>5</sup>: 62-63. 1923.

**Ames, O.** Additions to the orchid flora of Central America. Sched. Orchid. 4: 1-60. f. 1 + pl. 2, 3. 4 My 1923.  
1 genus and 40 species described as new.

**Ames, O.** New or noteworthy orchids. Sched. Orchid. 6: 1-99.  
f. 1-12. 3 N 1923.  
Many species described as new.

**Ames, O.** Notes on New England orchids—I. *Spiranthes*. Rhodora 23: 73-85. f. 1-4 + pl. 127-129. 28 Ap 1921.

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[Edward Willet Dorland Holway, born 8 My 1857, died 31 Mr 1923.]

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Studies on the pathogenicity, morphology, and cytology  
of *Nematospora Phaseoli* \*

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(WITH PLATES 7-9)

INTRODUCTION

As a group, the yeasts have been regarded primarily as typical saprophytes which set up fermentation changes by the action of their enzymes upon carbohydrate materials. However, the classic paper of Metchnikoff ('84) on phagocytosis describes a yeast parasitic on the crustacean *Daphnia*, and more recently certain yeasts have been found to cause disease in plants.

Our knowledge of the cytology of the yeasts is based on the studies of comparatively few investigators, whose results have been to a large extent contradictory.

My studies have been directed (1) to the morphology and phylogenetic relationships of the group of yeasts with slender elongated ascospores; and (2) to the cytology of the ascus in *Nematospora Phaseoli*.

MORPHOLOGY AND PHYLOGENETIC RELATIONSHIPS OF  
THE GENUS NEMATOSPORA

The genus *Nematospora* is one of a series of yeast genera which are characterized by long needle-shaped ascospores. This series of genera includes *Nematospora*, *Monospora*, and *Coccidiascus*. Whether such a series represents a phylogenetic unit is difficult to determine; but this is strongly suggested by the

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morphological characteristics of these genera. Moreover, the similarity of their habitats is very suggestive.

The genus *Nematospora* was created by Peglion in 1897, when he described the species *N. Coryli*. This species, according to Peglion, multiplies by budding in the cotyledons of hazel nuts and upon solid culture media, and produces asci from individual bud cells. In liquid media budding ceases and a sterile mycelium is produced. The asci are cylindrical, 65-70 microns long by 6-8 microns wide, and contain eight needle-shaped ascospores arranged in groups of four in each half of the ascus. The ascospores are one-celled, 2-3 microns wide by 38-40 microns long, and are equipped with a long flagellum-like appendage at one end. This appendage disappears during germination and the ascospore assumes the form of a short cell that may produce buds at both extremities.

The species *N. Lycopersici* described by Schneider ('16) from tomato fruits, although agreeing with *N. Coryli* in its most essential characteristics, differs from it in certain respects. In *N. Lycopersici* the asci, according to Schneider, arise from a conjugation of two bud cells, and there is evidence that they may develop from single cells, especially in vigorously growing cultures. The ascospores agree in general in their structure and method of germination with those of *N. Coryli*.

Nowell ('17) described what he considered as four further species of *Nematospora*. He designated these as *A*, *B*, *C*, and *D*. *Species A* and *B* in my opinion should not be regarded as species of *Nematospora*. They never multiply by budding, according to Nowell, and their so-called sporangia contain a very large number of spores which show a wide divergence in size and other characteristics from the ascospores of *Nematospora*. As Nowell points out, *Species B* agrees closely with the description of *Eremothecium Cymbalariae* as given by Borzi and Arnaud, and I believe he is justified in considering it the same or a very closely related species. The agreement is most marked in the matter of the number and arrangement of the spores in the so-called sporangium. Nowell's *Species C* and *D* bear a very close resemblance to the *Nematospora* species of Peglion and Schneider, and in my opinion clearly fall under the genus *Nematospora*. The ascospores are formed in two equal bundles in the opposite halves of the ascus. They possess the general characteristics of

the ascospores of *Nematospora Coryli* and *N. Lycopersici*, including the whip-like appendage. In germination the upper half of the ascospore (remote from the appendage) takes no visible part in the process. Nowell denies the existence of a septum at the middle region of the ascospore and yet he states that at the time of germination the ascospore wall just below its middle region swells into a sphere, from which germination takes place. This germination may be in the form of a germ tube or in the form of yeast-like budding, depending upon the conditions under which the ascospores are germinated.

The asci in *Species C* are intercalary in the cells of the hyphae. In *Species D* the asci may be formed by growth of the cells of the hyphae, but they are usually produced from single bud cells. The ascospores in this species sometimes germinate directly into asci. The thallus of *Species D* is typically yeast-like, whereas that of *Species C* is a dichotomously branched mycelium.

The genera *Monospora* and *Coccidiascus* have certain characteristics in common with the genus *Nematospora*. *Monospora bicuspidata*, \*the only species of this genus, was described by Metchnikoff ('84) from the body cavity of a *Daphnia* species, where it multiplies as a yeast. Its long cylindrical asci arise from the individual yeast cells and contain a single needle-shaped ascospore. The germination is like that in *Nematospora*, that is, a chain of yeast cells is produced from the middle region of the ascospore. The ascospores are apparently one-celled.

*Coccidiascus Legeri* multiplies by ordinary yeast budding and lives as a parasite in the intestinal cells of *Drosophila funebris*. The banana-shaped asci apparently arise from the conjugation of two yeast cells, and contain eight needle-shaped ascospores

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\* This specific name was written, apparently through inadvertence, as *Monospora cuspidata* Metchn. by Zopf (Die Pilze, 1890) and the error has been perpetuated by Lindner, Saccardo, and others down to Guilliermond and Tanner ('20). It is explicitly stated by Metchnikoff ('84, p. 181) that he adopted the specific name *bicuspidata* because of the fact that the spores are pointed at both ends, and this original form of the name is confirmed by Madame Olga Metchnikoff in her biography of her husband, both in the French edition and in her English translation (London, 1921). As this is the sole species of the genus, there could be no valid excuse for changing the specific name. Metchnikoff's generic name is antedated by the algal genus *Monospora* Solier (1845) of the Ceramiales, but even in that genus no specific name resembling *bicuspidata* is recorded. EDITOR.

arranged side by side in a single group. The ascospores of this species, like those of *Monospora bicuspidata*, are one-celled and without an appendage.

Other organisms that resemble *Nematospora* in one or more points are *Eremothecium Cymbalariae* Borzi ('88) with slender spores arranged in two opposite bundles in the so-called sporangium; *Protascus subuliformis* Dangeard ('03) with long slender spores, and a somewhat similar arrangement in the so-called sporangium; *Endomyces capsularis* Schiønning ('03) with asci formed intercalary in the mycelium, and ascospores that germinate either by budding or by sending out a germ tube, or, under special conditions, by producing an ascus direct; and *Endomyces javanensis* Klöcker ('09) with asci that seem to form indifferently from yeast cells or at the expense of some cell in the mycelium, and ascospores that germinate either by budding or by forming a germ tube.

Five species of *Nematospora* have been described, namely, *N. Coryli* Peglion, *N. Lycopersici* Schneider, *N. Species C* and *D* Nowell, and *N. Phaseoli* Wingard. These species show a remarkably close similarity in all their morphological characteristics, and the few minor differences that exist may fall well within the limits of the variations of species. In the genus *Monospora*, with the species *M. bicuspidata* Metchnikoff, and in the genus *Coccidiascus*, with the species *C. Legeri* Chatton, one finds forms that are very similar, both in their yeast-like development and in the character of ascospores produced. I am, therefore, convinced that these genera as noted are closely related to the genus *Nematospora*.

The genera *Protascus* and *Eremothecium* bear some resemblance to the genus *Nematospora*, but they must be studied more critically before one can be justified in making a definite statement as to their taxonomic position.

We are now confronted with the question as to whether the genus *Nematospora* should be referred to the *Saccharomycetes*. Peglion ('97, '01) in establishing the genus, did not hesitate to assign it to the *Saccharomycetes*. Hansen ('04) however, placed it with the genus *Monospora*, and considered both genera as doubtful *Saccharomycetes*. Schneider agrees with Peglion as to the relationships of the genus; Nowell, on the other hand, regards the fruiting body of *Nematospora* as a sporangium, and for that

reason states that the genus should not be referred to the *Saccharomycetes*. Guilliermond ('12) places the genera *Nematospora*, *Monospora*, and *Coccidiascus* in the fifth group of his classification of the *Saccharomycetes*, and designates them as budding yeasts with uncertain affinities.

My cytological studies of *Nematospora Phaseoli* show that its spore bearing body is undoubtedly an ascus. It seems, therefore, that Nowell's argument against placing the genus under the *Saccharomycetes* may be disregarded. Furthermore, practically all of the characteristics of *Nematospora* find parallels in one or more genera of the *Saccharomycetes*. I thoroughly agree, then, with Guilliermond in referring the genera *Nematospora*, *Monospora* and *Coccidiascus* to the *Saccharomycetes*.

#### MORPHOLOGICAL STUDIES ON NEMATOSPORA PHASEOLI

My own observations confirm the general conclusions just indicated as to the characters and relationships of this group of yeast-like genera.

As previously described (Wingard, '22) *Nematospora Phaseoli* was isolated from diseased Lima beans (*Phaseolus lunatus*) from eastern Virginia in 1921. A number of isolations have been made from Lima beans from different parts of Virginia and some of these isolations have been maintained in pure culture for more than three years. Monospore cultures were obtained by the use of the Barber pipette, and all reasonable precautions have been taken to keep the cultures pure.

#### METHODS

Beer wort agar\* has been most generally used in my culture studies of *Nematospora Phaseoli*. For poured plates and slants 10 to 15 cc. of this medium were employed. In the study of giant colonies 50 cc. were placed in 150 cc. Erlenmeyer flasks. The vegetable slants were cut out with a three-eighths inch cork

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\* Beer wort agar is prepared as follows: Soak 200 grams of crushed malt in a liter of cold water and slowly heat to a temperature of 60° C. Shake once in a while and after 45 minutes add 4 grams of hops; boil for an hour and filter. Add distilled water to make the filtrate up to a liter and then add 15 grams of agar agar, and gradually bring it into solution. Filter, and sterilize in autoclave at 15 pounds pressure for 20 minutes. The beer wort is the same as the above minus agar agar.

borer. All vegetable material was sterilized in the autoclave at 15 pounds for 20 to 30 minutes, with the exception of tomato fruits which were used uncooked.

Beer wort agar and fresh slants of garden beet, sweet potato, Irish potato, turnip, radish, carrot, parsnip, and green snap bean pods are very favorable media for both vegetative growth and ascospore formation. Sliced ripe tomato gives a fairly good growth. Whey agar, beef peptone agar, Czapek agar, corn meal agar, and Pfeffer's nutrient solution, with or without sugar, plus 1.5 per cent agar are very poor media. Of the liquids tested, beer wort, tap water and distilled water were found to give the best development. Pfeffer's nutrient solution gave no growth at all.

The vegetative phase of this species is typically yeast-like as a rule, but under certain conditions a mycelium is produced.

On beer wort agar plates at a temperature of 28 to 30° C., the colonies appear in 36 to 48 hours. They are convex, circular, with entire margins and smooth surface, opaque, dull. The internal structure is finely granular. The colony is cream colored at first but gradually turns brown with age. The maximum diameter of the colony is about 18 mm. and is attained in four to seven days. Asci and ascospores are produced in great numbers in 48 to 72 hours. After about a week the colony becomes surrounded by a border of mycelial growth, resulting from the germination of ascospores within the colony.

On beer wort agar slants, growth is abundant, slightly filiform in appearance, raised, dull, cream colored, opaque, contoured, with a butyrous consistency. The entire slant is covered in about a week. Mycelial branches develop on the sides of the test tube surrounding the margin of the slant. Giant colonies, grown on 50 cc. lots of beer wort agar in 150 cc. Erlenmeyer flasks, attain a diameter of 75 mm. in 30 days.

Growth in liquids is not so abundant as it is on solid media. In beer wort (solution) the growth is fairly slow but may apparently take place either on the surface or at the bottom of the liquid. In some cases a ring is formed on the sides of the test tube just at the surface of the liquid and the least jar is sufficient to cause the cells to settle to the bottom of the tube. In other cases the growth apparently takes place at the bottom of the tube, no development being visible at the surface of the solution.

The growth in beer wort is typically yeast-like, but occasionally short mycelial filaments can be found. Practically no asci and ascospores are developed.

In distilled water and also in tap water, a flocculent growth is made at the bottom of the liquid. This is composed almost entirely of mycelial filaments. Some are sterile and only rarely septate, while others are septate and bear intercalary asci which contain ascospores. The growth in very dilute beer wort is very similar to that in distilled water, but more yeast cells are produced than in the latter.

The organism produces a distinct alcoholic odor when grown in beer wort, and on beer wort agar and also on the vegetable media mentioned above.

The yeast cells multiply by budding, and it is not uncommon to see fifteen to twenty cells still attached to each other. The cells vary from a small ellipsoid type to large oval ones. The ellipsoidal cells measure from 5 to 14 microns by 2 to 10 microns and predominate in young cultures. The spherical cells measure from 10 to 20 microns in diameter and are very numerous in old cultures. They develop from the small ellipsoidal cells, and correspond to the arthrospores of Schneider.

Asci and ascospores are produced in great numbers in the cotyledons of Lima beans and also in favorable culture media such as beer wort agar or slants made from sweet potato, garden beet, etc. The asci arise from individual bud cells. They are cylindrical with rounded ends, 60-85 microns by 10-12 microns; ascospores eight, in two groups of four, 40-46 microns by 2.5-3 microns, slender, 1-septate, slightly ridged at septum, apex acute, base extended into a slender non-motile appendage about one and one-fourth times the length of the ascospore. In old cultures and sometimes under other conditions less than eight ascospores are formed in the asci.

#### TEMPERATURE RELATIONS

The minimum temperature for the growth of *N. Phaseoli* on beer wort agar is about 15° C.; the optimum, 25 to 30° C.; and the maximum, 40° C. The minimum temperature for ascospore formation is about 18° C.; the optimum, 25 to 30° C.; and the maximum, 34° C. Cultures grown at a temperature of 35 to 37.5° C. produce a fine type of yeast from the standpoint of its

budding. These cultures lose their spore-forming power if subjected to this temperature for a very long time. The same thing occurs when a culture is left too long before being transferred to fresh media. Two of my cultures were allowed to go for about a month on beer wort agar slants before being transferred. They lost the power to form spores in that short time. These cultures have been grown on various media for the last two years but not a single spore has been observed. They produce mycelium under the conditions described above, but they multiply primarily by budding as true yeasts.

#### PATHOGENIC YEASTS

The discovery of parasitism among the yeasts should perhaps be credited to the French physician, Dr. Maurice Raynaud ('69), who described and figured a yeast like organism, which he compares with *Oidium albicans* and *Saccharomyces Cerevisiae*, as regularly found in connection with the malady called black tongue. Raynaud raised the question as to whether the yeast actually caused the hypertrophy, but expressed the opinion that the latter merely furnished a condition favorable for the growth of the parasite. It is probably the same organism which was described as *Saccharomyces linguae-pilosae* by Lucet ('01) in an account of this disease. According to Guéguen ('09) and Thaon ('09), this yeast acts only in association with *Oospora lingualis*. There is said to be a symbiotic association between these two organisms.

Metchnikoff ('84) in the paper referred to above, reported the discovery of the yeast *Monospora bicuspidata* in the body cavity of a crustacean (*Daphnia*) causing a typically diseased condition. The transparency of this crustacean enabled Metchnikoff to follow with great accuracy the interrelation of host and parasite, and the entire process of infection. He thus made the memorable discovery of phagocytosis which has since played such an important rôle in medical science.

Since the appearance of Metchnikoff's report, numerous other yeasts and yeast-like fungi have been reported as parasites on both man and animals. *Endomyces albicans*, according to Guilliermond ('12), has been found to produce lesions in man. It is now supposed to be the causal agent of the disease known as thrush, and this or a similar organism has also been found in

lung infections by Simon ('17), Birch-Hirschfeld ('75) and Castellani ('13). Ashford ('15) in studying the etiology of the disease known as sprue has announced the constant presence of a yeast like organism in the digestive tract. He thus confirms and extends the results of Bahr ('14), Kohlbrugge ('01), Le Dantec ('08) and others, all of whom had previously isolated fungi of the *Oidium albicans* type from sprue patients. Ashford's organism was named *Parasaccharomyces Ashfordi* by Anderson ('17) who also isolated another species, similar in physiologic properties, but differing in morphologic characteristics. The yeast-like organism, *Cryptococcus farciminosus*, discovered by Rivolta ('73) and more thoroughly studied by Rivolta and Micellone ('83) as the cause of farcy or African glanders in horses and mules, has been discussed by several other investigators in southern Europe and Japan.

A number of yeasts have been described in tumors of various kinds. One of the most characteristic of these is the yeast *Saccharomyces subcutaneus tumefaciens*, described by Curtis ('96) from a tumor of the hip and also from a lumbar abscess in man. *Saccharomyces parasitarius* was described by Trabut ('91) from the grasshopper *Acridium perigrinum* upon which it is a parasite. The yeast *Coccidiascus Legeri* was described by Chatton ('13) as an active parasite in *Drosophila funebris*. *Cryptococcus Anobii* was discovered by Escherich ('00) in the cells of the intestinal wall of the larva of *Anobium paniceum*. *Saccharomyces apiculatus parasiticus* has been described by Lindner ('95) from the body of *Aspidiotus nerii*, and a very similar species causes a fatal disease among caterpillars. *Saccharomycopsis guttulatus* has been studied by Buscalioni ('96) and Wilhelmi ('98). It seems to live as a true parasite in the intestinal canal of birds, reptiles, and mammals. These cases may serve to give a general conception of the pathogenicity of yeasts and yeast-like fungi in relation to animals. A somewhat extended review of the earlier work in this field is to be found in a paper by Vuillemin ('01).

Peglion ('97) was the first to report a parasitic yeast on plants. He described a yeast from diseased hazel nuts in Italy, and created the genus *Nematospora*, species *Coryli*, for it. Schneider ('16) described a second species of this genus, *Nematospora Lycopersici*, from diseased tomato fruits in California.



Nowell ('15) isolated four fungi from diseased cotton bolls in the British West Indies during the seasons of 1915 and 1916. These fungi were described by Nowell ('17), and designated as *Species A*, *B*, *C*, and *D*. He considered them as closely related forms and states that *Species C* and *D* are clearly related to the *Nematospora* species described by Peglion and Schneider. According to Nowell ('17), M. S. F. Ashby, sometime microbiologist in the Jamaica Department of Agriculture, independently discovered *Species A* and *B* in cotton bolls in Jamaica; and Bartlett ('07), Government botanist in British Guiana, obtained *Species A* from cotton bolls, and probably saw the spores of *Species C* or *D* in that country in 1907.

*Eremothecium Cymbalariae*, a fungus considered by Nowell as agreeing exactly with his *Species B*, was described by Borzi ('88) in Italy as a parasite on the capsules of *Linaria Cymbalaria*. This fungus was redescribed by Arnaud ('13) in France as a parasite on the fruits of *Cachrys laevigata*. It should be noted at this point that Arnaud described and figured two types of fruiting bodies and spores from his cultures. His macrosporangia and macrospores closely resemble the asci and ascospores of Peglion's *Nematospora Coryli*. He no doubt had a mixed culture.

*Nematospora Phaseoli* was discovered by the writer ('22) in diseased Lima beans from eastern Virginia in 1921, and since that time it has been found to occur more or less generally in fourteen Virginia counties. It has been found once in Lima beans from Tennessee and several times in Lima beans from Alabama. Anderson ('24) also found this species in Lima beans in Illinois in 1923. The frequency, therefore, with which this species is found in Virginia and Alabama indicates that it is of rather general occurrence in those states; and it is believed that a more careful survey will reveal its presence in other Southern States.

The several species of *Nematospora* and *Nematospora*-like fungi have now been found in the fruits of a considerable variety of plants. The hosts as reported thus far are shown in Table 1.

The leguminous plants are predominant in the list, and with the exception of cotton and tomato are the most important from an economic standpoint. My studies indicate that the small Lima or Sieva bean is the most susceptible host for *Nematospora Phaseoli*. The larger types of Lima beans are susceptible but,

as a rule, the infection is less severe. Infection of Bird-eye beans, Black-eye cowpeas and sweet potato has been observed but once. It should be noted, nevertheless, that the Bird-eye bean and cowpea seed showed a high percentage of typical infection and the sweet potato showed an abundant growth of the yeast. No difficulty was experienced in isolating *Nematospora* from these specimens. In pure culture these forms appear to be identical with that from the Lima bean.

TABLE I.—HOST PLANTS OF *Nematospora* AND *Nematospora*-LIKE FUNGI

Host	Pathogen
<i>Corylus avellana</i> (Hazel bush) . . . . .	<i>N. Coryli</i> Peglion
<i>Lycopersicum esculentum</i> (Tomato) . . . . .	<i>N. Lycopersici</i> Schneider
<i>Lycopersicum esculentum</i> (Tomato) . . . . .	Species A, B, D, Nowell
<i>Phaseolus lunatus</i> (Lima bean) . . . . .	<i>N. Phaseoli</i> Wingard
<i>Phaseolus lunatus</i> (Lima bean) . . . . .	Species D, Nowell
<i>Phaseolus vulgaris</i> (French bean) . . . . .	Species D, Nowell
<i>Phaseolus vulgaris</i> (Bird-eye bean) . . . . .	<i>N. Phaseoli</i> Wingard
<i>Ipomoea Batatas</i> (Sweet potato) . . . . .	<i>N. Phaseoli</i> Wingard
<i>Vigna catjang</i> (Rounceval cowpea) . . . . .	Species A, D, Nowell
<i>Vigna sinensis</i> (Black-eye cowpea) . . . . .	<i>N. Phaseoli</i> Wingard
<i>Dolichos Lablab</i> (Bonavist) . . . . .	Species D, Nowell
<i>Canavalia gladiata</i> (Sword bean) . . . . .	Species D, Nowell
<i>Crotalaria retusa</i> . . . . .	Species D, Nowell
<i>Crotalaria juncea</i> (Sunn hemp) . . . . .	Species D, Nowell
<i>Tephrosia</i> spp. . . . .	Species D, Nowell
<i>Indigofera</i> spp. . . . .	Species D, Nowell
<i>Cassia</i> spp. . . . .	Species D, Nowell
<i>Gossypium</i> spp. (Annual & perennial cottons) . . . . .	Species A, B, C, D, Nowell
<i>Ricinus communis</i> (Castor oil bean) . . . . .	Species D, Nowell
<i>Jatropha urens</i> . . . . .	Species D, Nowell
<i>Momordica charantia</i> (Coolie pepper) . . . . .	Species D, Nowell
<i>Asclepias curassavica</i> . . . . .	Species D, Nowell
<i>Citrus sinensis</i> (Sweet orange) . . . . .	Species D, Nowell
<i>Linaria cymbalaria</i> . . . . .	<i>Eremothecium Cymbalariae</i> Borzi
<i>Cachrys laevigata</i> . . . . .	<i>Eremothecium Cymbalariae</i> Borzi
<i>Cachrys laevigata</i> . . . . .	<i>N. Coryli</i> Peglion (?)

## SEVERITY OF INFECTION AND ECONOMIC IMPORTANCE

As shown in the table above, the fungi of the *Nematospora* type are capable of infecting the fruits of a wide range of plants. A brief summary of the reports given by various authors shows

the economic importance of these diseases. Peglion, for instance, states that he examined a large number of hazel nuts in Italy during the seasons of 1897 and 1901 and a fairly high percentage of spoiled nuts was found. He reports one case in which 25 per cent of the nuts were spoiled. Schneider had no opportunity to determine the extent of injury on tomato fruits because he was uncertain as to the source of the affected fruits. Nowell, on the other hand, finds *Nematospora* infection fairly common on tomatoes in the British West Indies. There is evidence, therefore, that infection is not uncommon on tomatoes in the tropics. The results of Nowell's studies show also that the *Nematospora* diseases are of considerable economic importance on the fruits of many other plants in the British West Indies. The losses in the case of cotton often run as high as 20 per cent in the early picking season and increase to almost 100 per cent for the late picking season. Nowell states, however, that the prevalence of infection is much greater in some islands than in others, and much greater in some seasons than in others.

My observations have been limited to cases of infection of Lima beans (*Phaseolus lunatus*), Bird-eye beans (*Phaseolus vulgaris*), Black-eye cowpeas (*Vigna sinensis*), and sweet potato (*Ipomoea Batatas*). Of these hosts, the small Lima or Sieva bean is the most severely affected. Infection of the large seeded varieties of Lima beans is, as a rule, slight as compared with that of the Sieva type with small seed. Cases of infection range from those in which only small spots are produced to those extreme cases in which the entire seed is involved. In York County, Virginia, where the disease is most common, several-growers have experienced such heavy losses that they no longer attempt to grow the Sieva bean. Losses have been found to range from a trace to 90 per cent of the crop, but, as a rule, they do not exceed 10 to 20 per cent. Although infection is slight during the early part of the season, it becomes very severe during August and September.

My observations of infection on the other hosts named above have been too limited to justify any definite estimate of the losses sustained, but the cases observed indicate that these hosts are subject to severe injury. It seems that the underground habitat of the sweet potato should protect it against infection

in the field, but *Nematospora* may prove capable of producing a storage rot. Its luxuriant growth on sliced sweet potato suggests this as a possibility, but whether this actually is the case remains at present only a matter of conjecture. When one takes into consideration the wide range of its distribution and the large number of hosts, together with the severity of infection, *Nematospora* must be recognized as a parasite of considerable economic importance.

### INFECTION STUDIES

Peglion obtained no decisive results in inoculating the mature cotyledons of hazel nuts with *Nematospora Coryli*. Schneider apparently made no inoculations on tomato fruits with *Nematospora Lycopersici*. Nowell made a number of inoculations on green cotton bolls with *Nematospora* (*Species D*), and succeeded in getting infection when the bolls were punctured with a needle which had been previously dipped into an agar culture of the organism.

Infection with *Nematospora Phaseoli* has been obtained repeatedly on Lima beans of the small Sieva type under both greenhouse and field conditions. Atomizing the young pods with an aqueous suspension of the organism failed to produce infection. Negative results were also obtained when uninjured pods were smeared with a pure culture of the organism; but infection was readily produced in the seed when the pods were punctured with a fine needle, previously dipped into a pure culture of the yeast. The pods were carefully washed with a 1 to 1000 bichloride solution and allowed to dry before being punctured. Inoculations made in this manner resulted in infections that closely resemble those that occur under natural conditions. The characteristic symptoms were evident within two to three days after inoculation, and were quite conspicuous within seven to ten days.

Similar inoculations failed to produce infection of garden beans (*Phaseolus vulgaris*). Tomato fruits growing in the greenhouse were also inoculated but no infection occurred. It was found, however, that ascospores were formed in the fruits that were allowed to become thoroughly ripe. The sliced ripe fruits make a fairly good medium for the growth of the organism. Inoculations were made on another series of green tomato fruits

growing in the greenhouse. Three species of *Nematospora* were employed in this experiment; namely, *N. Phaseoli* from Lima bean, *N. Sp. D.*, Nowell, from cotton, and *N. Sp. D.*, Nowell, from tomato. Eighteen fruits were inoculated, six with each culture; and each fruit was punctured at six different points, making a total of thirty-six inoculations with each species.

These fruits were examined as soon as they were thoroughly ripe, but the organism was found in only one of them. This proved to be one of those that had been inoculated with *Sp. D.*, Nowell, from tomato. The puncture had healed over, but in a small area near the surface of the fruit the organism was still present. The other punctures appeared the same as those in the controls. The temperature, which is no doubt an important factor in infection, was lower in the greenhouse than it usually is in the field during the summer months and this probably had some influence on the results obtained.

#### THE RÔLE OF INSECTS IN INFECTION

Peglion states that *Nematospora* lesions on young hazel nuts are mostly near the micropyle, and expresses the opinion that the parasite enters by way of the style before the pericarp becomes woody. This may be true but the type of lesion described by him on the cotyledons of the hazel nut strongly suggests insect punctures as the portal of entry. Nowell ('17, '20) and his associates have found that *Nematospora* infection in cotton bolls and the fruits of many other plants is accomplished only by the punctures of certain insects; namely, the cotton stainer (*Dysdercus delauneyi*), the green bug (*Nezara viridula*), the leaf-footed tomato bug (*Leptoglossus balleatus*), and the red tomato bug (*Phthia picta*). The first two are the most important.

Natural infection of Lima beans and cowpeas with *Nematospora Phaseoli* in my experience is apparently entirely dependent upon the puncture of the green bug (*Nezara hiliaris*\*). This insect is always present wherever infection occurs, and the lesions on the cotyledons always develop around its punctures. The severity of infection depends directly upon the number of insects present; and this fact, together with high temperature,

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\* Specimens of this insect were identified by Dr. Herbert Osborn of Ohio State University in 1923.

explains why the percentage of infection is so high during the latter part of the season.

*Nezara viridula*, an insect almost indistinguishable from *Nezara hiliaris*, feeds upon pecans in the Southern States and produces a disease known as kernel-spot. The lesions of this disease are so similar to those of *Nematospora* infections on the fruits of other plants that the writer at one time was of the opinion that perhaps *Nematospora* was associated with the kernel-spot disease. The fact, too, that kernel-spot is most severe in groves where cowpeas are grown as a cover crop supports this view. With these facts in mind, several lots of affected pecans from Georgia were examined but *Nematospora* was not found. Platings were also made from some of the most typical lesions, but *Nematospora* failed to develop.

#### INSECTS AS CARRIERS OF INFECTION

The cotton stainer (*Dysdercus delauneyi*), the green bugs (*Nezara viridula* and *Nezara hiliaris*), the leaf-footed tomato bug (*Leptoglossus balteatus*), and the red tomato bug (*Phthia picta*) are so closely associated with *Nematospora* infection on the various hosts that they appear to be carriers of infection. To test this point, Nowell collected *Dysdercus delauneyi*, *Nezara viridula*, *Leptoglossus balteatus* and *Phthia picta* from fields where *Nematospora* infection was common on cotton and placed them on caged plants with healthy bolls. The punctures made by these insects into the caged bolls resulted in typical *Nematospora* infection in the majority of cases, and an examination revealed the presence of the organism. According to Nowell, *Edessa mediatubunda* also feeds on cotton bolls and the fruits of many other plants in the British West Indies, but he has never succeeded in getting infection from its punctures on caged plants.

I have conducted similar experiments with *Nezara hiliaris*. Specimens of this insect were collected from gardens where *Nematospora* infection was present on Lima beans and were transferred to another section and placed on caged plants with disease-free pods. The pods on these plants when examined two weeks later showed numerous punctures and the punctured seed showed typical infection. The organism was readily found in the lesions around the punctures.

These results indicate that *Nematospora* is carried by the

above named insects, but whether it is carried internally or externally remains to be determined. Nowell has attempted to isolate it from *Dysdercus delauneyi* and *Nezara viridula* but without success, and I have had the same experience with *Nezara hiliaris*. Other yeasts and yeast-like fungi are very readily obtained from this insect, but I have consistently failed to isolate *Nematospora Phaseoli*. I am inclined, nevertheless, to believe that these insects are themselves infected with the organism. The negative results obtained thus far are very probably due to improper technique.

#### THE RELATION OF HOST TO PARASITE

Infection is apparently restricted to the fruits of the several hosts of *Nematospora*, not a single case being reported as yet where any other portion of the plant is affected. This suggests that infection is dependent upon the presence of an abundant supply of available carbohydrates, such as is found in fruits and in the fleshy cotyledons of certain seeds.

My studies of *Nematospora Phaseoli* have shown that infection may occur at any time during the development of the Lima bean seed, but in order to cause much injury it must take place before the seed is half grown. In case of early infection the seed may either be killed outright or only severely stunted in its development. If infection occurs near maturity only small lesions are produced on the cotyledons and the seed is not materially injured. In the majority of cases the testa remains intact and the affected region is wrinkled, somewhat sunken and of a dark-brown color. In rare cases the testa is ruptured at the point of infection and a crater-like lesion is produced on the surface of the cotyledon. The affected tissues are collapsed, grayish-brown in color and granular in texture. The cells in the affected region apparently are low in starch content.

#### CYTOLOGY OF THE YEASTS

Although our knowledge of the cytology of the yeasts has been greatly advanced during the last quarter of a century, it is still on a rather unsettled basis. The much discussed problem as to whether or not yeast cells possess a typical nucleus has finally been answered in the affirmative, but beyond this point our knowledge is quite vague. There is, however, considerable

divergence in this respect between the widely different groups now included under the general conception of the yeasts. Of these groups, the cytology of that of *Schizosaccharomyces* is most completely understood.

The exact method of nuclear division may be said to be a matter of dispute for all yeasts. Some investigators contend that it is always amitotic; others are of the opinion that it is amitotic at the time of budding and mitotic in the ascus during ascospore formation; while still others contend that it is mitotic for both processes. Furthermore, such points as the type of spindle, presence or absence of astral rays, centrosomes, chromosomes, etc., for most yeasts remain as yet practically untouched. Then, too, our knowledge of the nuclear phenomena involved in the origin of the ascus and the manner of ascospore formation cannot be regarded as settled yet for any single yeast.

#### PRESENCE OF A NUCLEUS

Following the discovery of the cell nucleus by Robert Brown in 1831 and Meyen in 1826, and the development of the conception of protoplasm by Von Mohl in 1846, and others, the cellular make-up of the common brewers' yeast (*Saccharomyces Cerevisiae*) was an object of considerable study, particularly as to whether its cells have a nucleus. We can recognize in this connection two groups of observers: (1) those who, like Nägeli ('44), Schleiden ('49), Schmitz ('79), Strasburger ('84, p. 158, f. 77), Zalewski ('86), Hansen ('86), Zacharias ('87), Moeller ('92, '93), Janssens and Le Blanc ('98), Dangeard ('93, '94), Buscalioni ('96), Maffucci and Sirleo ('95), Hofmeister ('00), Bouin ('98), Errera ('98), and Hirschbruch ('02), reported as nuclei granules or bodies in various positions in the yeast cell; and (2) those who, like Krasser ('85), Hieronymus ('93), Stecksén ('01), and Wager and Peniston ('10), reported chromatic granules or other aberrant structures as substitutes for the nucleus. Brücke ('98), Raum ('91), and Macallum ('95) denied the existence of nuclei in the cells of brewers' yeast. The more recent studies of Guilliermond ('02), Swellengrebel ('05), Fuhrmann ('06), and others have shown that the yeast nucleus in all of its general characteristics is comparable to that of the higher fungi.



## DIVISION OF THE NUCLEUS

On the question as to whether the reproduction of the yeast nucleus is by direct or indirect division, we can again distinguish, as noted above, several classes of contentions in the literature: (1) those of Dangeard, Hofmeister and others, who hold that nuclear division is direct at the time of budding; (2) those of Janssens and Le Blanc, and Bouin, who hold that it may be either direct or indirect for budding, but is always indirect for ascospore formation; (3) those of Swellengrebel, and Fuhrmann, who hold that it is indirect for budding; (4) those of Hirschbruch, who holds that it is indirect for both budding and ascospore formation; (5) those of Wager and Peniston, and Kohl ('07), who hold that it is direct in both budding and ascospore formation; and (6) those of Guilliermond, and Buscalioni, who contend that it is direct for budding and indirect for ascospore formation.

## EXISTENCE AND NUMBER OF CHROMOSOMES

Wager ('98) studied nuclear division in the asci of *Saccharomyces Cerevisiae*, *S. Ludwigii*, and *S. pastorianus*, and observed deeply stained granules which he was inclined to call chromosomes; but in 1910 he and Peniston, after repeating these studies, make the following statement: "We are not now inclined to lay any stress upon the suggestion (Wager, 1898) that the chromatic granules are chromosomes. The whole process appears to be one of direct division or fragmentation, in which nothing in the nature of a spindle figure or definite chromosomes can be observed."

Swellengrebel ('05) studying the nuclei of compressed yeast cells (*S. Cerevisiae*) at the time of budding, gives the chromosome number as four. He describes what he calls an achromatic spindle and what he considered to be centrosomes. The four chromosomes arrange themselves on the equator in the form of a ring while the karyon is being transformed into the spindle. The chromosomes divide and four pass to each pole of the spindle where the two daughter nuclei are reconstructed. Fuhrmann ('06) a few months later, confirmed Swellengrebel's results. He studied nuclear division in the budding cell of *S. ellipsoideus*. He reports the existence of an achromatic spindle with a centrosome at each pole. He also gives the chromosome number as

four, and states that these divide, giving four daughter chromosomes for each of the daughter nuclei.

Guilliermond ('17) reported the results of his studies on the nuclear division in the ascus of *Schizosaccharomyces octosporus*. He states that this species is much more favorable for cytological study than other yeasts. He was able to demonstrate chromosomes and an achromatic spindle with centrosomes but found the chromosomes too small to permit of an accurate count; nevertheless, he figures about four or five passing to each pole of the spindle during the late anaphase. He states that his studies on *S. Cerevisiae* and *S. ellipsoideus* have demonstrated that the pretended mitotic figures described by Swellengrebel and by Fuhrmann resulted from an erroneous interpretation of the vacuole and granular material contained in it, or in the cytoplasm.

#### CONJUGATION AND ASCUS FORMATION

Schiønning ('95) described the ascus of *Schizosaccharomyces octosporus* as resulting from the conjugation of two sister cells, and Hofmeister ('00) described a nuclear fusion in the conjugating cells. Guilliermond ('01) confirmed Hofmeister's observations. He described the ascus of *S. octosporus* as arising from the conjugation of two identical cells lying side by side in the same colony. The cells become united by a conjugation canal formed by the fusion of two outgrowths from the gametic pair. The wall separating the tips of the tubes is dissolved and the two nuclei of the conjugating cells migrate into the conjugation canal and fuse to form the primary nucleus of the ascus. The ascus increases in volume while its nucleus undergoes two, or sometimes three, successive karyokinetic divisions, which gives four or eight nuclei for the ascospores. Guilliermond found also that the ascus in this species sometimes originates from a single cell. In that event, two cells become united by a conjugation canal but the separating wall remains intact, and each cell develops into an ascus.

Guilliermond ('02) showed that the asci of *Schizosaccharomyces pombe* and *S. Mellacei* arise in the same manner as described for *S. octosporus*. In these species, however, the asci more frequently arise from single cells. It may be the result of the failure of the separating wall between the two cells to be

reabsorbed, or a single cell may develop into an ascus without even attempting to conjugate with another. Šulc ('10) described a conjugation in the ascus formation of *S. Aphalarae calthae* which appears to be analogous to that of *S. octosporus*. Nakazawa ('14) is reported by Guilliermond and Tanner ('20) as having described a similar process in the ascus formation of *S. santawensis* and *S. formosensis*.

An isogamic conjugation is also known to occur in the ascus formation of the budding yeasts, especially in the genus *Zygosaccharomyces*. Barker ('01) described it for *Z. Barkeri*, and Pearce and Barker ('08) described it for *Zygosaccharomyces F.* An analogous process has been described for *Z. priorianus* and *Z. mandshuricus* by Klöcker ('05), for *Z. javanicus* by de Kruyff ('08) for *Z. japonicus* by Saito ('09), for *Z. lactis* by Dombroski ('10), and for *Z. major* by Takahashi and Yukawa ('12). Certain of these authors state that asci may also arise from single cells in the species which they studied.

An isogamic conjugation has also been described in the ascus formation of certain other genera. Chatton ('13) for example, described it for the yeast *Coccidiascus Legeri*, and Schneider ('16) reported it for *Nematospora Lycopersici*. Schneider, however, states that there is evidence that the asci of *N. Lycopersici* may develop from a single cell.

In addition to the type of conjugation described above, certain authors have described processes which they consider to be heterogamic. Pearce and Barker ('08) described a yeast which they designated as *yeast G* in which the conjugation tends towards heterogamy. Guilliermond ('11) described what he considers to be a strictly heterogamic process in the yeast *Zygosaccharomyces Chevalieri*. The asci in this species result from the conjugation of two cells of different dimensions. The contents of the small cell pass into the large one through the conjugation canal. The large cell separates itself from the small one by means of a wall, and later develops into the ascus. Guilliermond ('18) described the same type of conjugation for *Z. Nadsonii*, and in a paper of the following year ('19) for *Z. Pastori*. In these species conjugation occurs between a mother cell and an incompletely developed daughter cell, the mother cell in this case playing the part of the female gamete, while the daughter cell functions as the male.

Klöcker ('06) found that the conjugation in *Z. priorianus* in some cases was isogamic but in others it was heterogamic, occurring between a mother cell and a bud still attached. He also found that many cells formed ascospores without undergoing conjugation. Guilliermond ('11) described the same types of conjugation for *Debaryomyces globosus*, and Konokotina ('13) for *D. tyrocola*. Nadson and Konokotina ('12) found that the conjugation in the species *Nadsonia fulvescens* and *Nadsonia elongata* always takes place between a mother cell and a bud formed by it. The contents of the bud pass into the mother cell, which, instead of developing directly into an ascus, gives birth, by budding, to a new cell into which its contents are poured; and this cell develops into an ascus.

In certain yeasts such as *S. Ludwigii*, *Willia Saturnus* and yeast *Johannisberg II* the asci develop from single cells, but the ascospores as a rule conjugate two by two at the time of germination. This phenomenon was first described by Hansen ('91) in *S. Ludwigii*. The ascospores become united by means of a conjugation canal into which the nucleus and cytoplasm of each pass, and in which nuclear fusion occurs. A zygosporangium is formed which later germinates by sending out a germ tube from which numerous vegetative cells are produced by budding. About one-fourth of the ascospores of this species germinate without any sign of conjugation. Guilliermond ('03) found that the conjugating ascospores in this species as well as in *Willia Saturnus* often germinate into asci instead of producing vegetative cells. The single ascospores were found to do the same thing. Hansen ('91) showed that the ascospores of *S. Cerevisiae* and "*Johannisberg II*" would also, under certain conditions, germinate directly into asci either with or without conjugating. Marchand ('13) described a similar conjugation of ascospores in *S. intermedius*, *S. turbidans*, *S. validus*, *S. ellipsoideus*, *S. Vini Muntzii*, *S. Willianus*, *S. Bayanus*, and "*Johannisberg I*." Guilliermond ('17b) described a yeast from pulque in which the asci develop from single cells. The ascospores conjugate two by two at the time of germination and in unfavorable solid culture media change directly into asci. This species, like *S. Ludwigii* and *Pichia membranaefaciens*, often forms a mycelium on the surface of old cultures. In that case, each cell in the mycelium may develop into an ascus with the normal number of ascospores.

## NUMBER OF ASCOSPORES

The number of ascospores contained in the ascus of various yeasts runs from one to eight. The number is usually fixed in any one species or at least a certain number is found to predominate. In *Monospora bicuspidata*, *Nadsonia fulvescens*, *Nadsonia elongata*, *Debaryomyces tyrocola* and others, a single ascospore is produced. In *Schwanniomyces occidentalis*, *Debaryomyces globosus*, *Zygosaccharomyces Nadsonia*, one to two ascospores are produced, with one predominating. The ascus of *Z. bisporus* contains two ascospores as a rule. In *Saccharomyces Cerevisiae* the number varies between one and five, but the number four is more frequent. In *S. pastorianus* the same variation in number obtains but the number two predominates. In *S. Ludwigii* and the yeast *Johannisberg II*, the number is almost always four. In *Schizosaccharomyces octosporus* the number is either four or eight. In *S. Mellacei* and *S. pombe* the number is invariably four. In *Nematospora Coryli*, *N. Lycopersici*, and *Coccidiascus Legeri*, the number is almost always eight. The variation in number of ascospores within a genus is apparently very little greater than that of a single species.

## METHOD OF ASCOSPORE FORMATION

As previously noted, the real nature of ascospore formation in the yeasts is none too well understood. Are the yeast ascospores cut out by free cell formation, or are they formed by cleavage? Wager ('98) describes the spores of *S. Cerevisiae* and *S. Ludwigii* as lying free in the protoplasm of the ascus. The spores are said to be at first very small, but they gradually increase in size at the expense of the surrounding protoplasm, a thick cell-wall being produced around each, until finally they completely fill the mother-cell.

Janssens and Le Blanc ('98), describing the process in the same species, write: "Pour compléter les spores, les noyaux s'entourent d'une partie plus dense de protoplasme, autour de laquelle une membrane se forme librement sans la participation de la membrane de la cellule-mère. L'apparition de cette membrane peut surtout s'étudier, quand il ne se forme que deux spores, mais on peut encore en poursuivre tous les détails, dans des cas de très bonne fixation, sur des cellules produisant quatre

spores. Il se forme une sorte de plaque cellulaire librement dans le protoplasme à une certaine distance du nucléole. Les trabécules du protoplasme se régularisent et bientôt, par le dépôt d'une substance squelettique analogue à la cellulose, on voit apparaître dans le protoplasme une zone circulaire plus réfringente entourant un protoplasme très dense."

Guilliermond ('02) has studied ascospore formation in a large number of yeasts, and has described the presence of spore plasm and epiplasm as in the asci of the higher Ascomycetes. He is of the opinion, too, that the ascospores are formed by free cell formation, but he states that the figures are too small to allow one to follow the details of the process.

#### CYTOLOGY OF NEMATOSPORA PHASEOLI

The material used in this study was grown in pure culture on either beer wort agar or sweet potato slants. Cultures ranging from one to ten days old were used in order to obtain all of the different types of cells and stages in the development of the organism. Cultures one to three days old were found to supply excellent material for the study of the development of the asci and ascospores; those three to five days old were very good for ascospore germination; and those from five to ten days old supplied excellent material for the study of the direct germination of the ascospores into asci, the conjugation of ascospores, and the formation of asci in the mycelial branches.

Numerous solutions were tested for killing and fixing the material; and, of those tested, Flemming's weak solution, diluted 1 to 200 with distilled water, was found to give the best results. This solution as a rule gave good fixation with little or no shrinkage. A small quantity of the culture material was transferred to about ten to fifteen drops of the fixing solution by means of a platinum loop. After the material had remained in the fixing solution for 15 to 30 minutes, it was mounted for staining by the stipple method, as described by Harper ('99) and others, for mounting germinating smut spores. The ether-celloidin method, as described by Davis ('22) for mounting germinating spores, was also used with very good success, especially when the material was stained with haematoxylin.

Several stains, including the majority of those recommended by the various authors who have studied the yeasts, were tested;

but Flemming's triple stain was the only one that gave satisfactory results. Haidenhain's iron-alum-haematoxylin was found to be very good for staining ascospores and resting nuclei, but otherwise it failed to bring out the details that are shown with the triple stain.

#### ASCOSPORES AND THEIR GERMINATION

The mature ascospores are comparatively very long and slender and consist of two cells of about equal length, with the basal one ending in a long whip-like appendage. When stained, the basal cell exhibits an alveolar cytoplasm and a single well defined nucleus, which consists of a deeply stained nucleole, a less densely stained chromatic reticulum, nuclear sap, and a nuclear membrane (FIGS. 18a, 18b). The nucleus is situated in the upper end of the cell near the septum which separates the ascospore into two cells, and tends to be slightly pointed in the region where the nucleole is located. The apical cell of the ascospore shows quite a different aspect. The cytoplasm in this cell, which apparently begins to disintegrate very early, appears in the form of densely stained clumps, and no nucleus can be distinguished.

At the time of germination, the upper region of the basal cell of the ascospore swells and becomes spherical in shape just below the transverse septum, the nucleus enlarges and divides to form nuclei for the cells that later bud off from this region. The nuclei at this stage are very small, about 2 microns in diameter; but I have observed in a very few cases a very minute spindle-shaped figure which appears to be similar to the undoubted mitotic figures that are found later in the ascus. The nucleus may divide either before or after budding is evident. In some cases it divides and two nuclei are found before budding begins (FIG. 17); in other cases a bud cell is well formed before nuclear division takes place (FIG. 15a). In still other cases, which seem rare, one large nucleus and two small ones are seen in the swollen region before budding occurs (FIG. 12), indicating perhaps that the division of the mother nucleus has been followed by the division of one of the daughter nuclei. The apical cell has never been observed to germinate; its contents undergo further disintegration and it remains as an apparently functionless appendage. The question as to its nucleus is discussed

below. From one to six chains of bud cells may be seen attached to the swollen region of the ascospore. These cells later become dissociated and may either bud as yeasts or develop into asci. The yeast cells contain a single nucleus (FIG. 19) which resembles that of the ascospore. Nuclear division has not been observed in these cells during budding.

In addition to the method as described above, the ascospore often exhibits several other modes of germination, the cause of which has not been definitely determined. I am inclined to believe that the budding type of germination as described above is the most common when fresh solid media are used, although it may occur under other conditions.

The second type of germination, which is characterized by the production of one or more germ tubes from the swollen region of the ascospore, occurs in liquids and also in old cultures on solid media. However, a sharp line of demarcation cannot be drawn between the conditions that are necessary for this and the first mode of germination. Two ascospores lying side by side in apparently the same environment may exhibit different types of germination; one by budding, and the other by germ-tube production. Furthermore, ascospores may be observed with a chain of bud cells attached to one side and a septate mycelial hypha extending from the other side. Then, too, the method of germination may be intermediate between budding and the production of germ tubes.

In the third type of germination the basal cell of the ascospore swells and develops directly into an ascus (FIG. 20). This occurs in old cultures on solid media after an abundant growth has been made. Whether this is due to toxic substances or to a lack of food, or both, has not been determined. We should note here the cases in which two adjacent ascospores produce conjugation tubes which fuse at their tips and develop into an ascus. This procedure seems to be rather unusual, and yet it has been observed several times in old cultures, especially on Irish and sweet potato slants. The drying out of the medium may also be an important factor in determining the type of ascospore germination.



## NUCLEAR PHENOMENA INVOLVED IN ASCUS FORMATION

As previously stated, the cells that are produced by budding at the time of ascospore germination become dissociated and either develop individually into asci or multiply further by budding. If budding occurs, the individual cells thus formed may in turn develop into asci. Since this seems to be the most common method of ascus formation, I shall begin by describing the nuclear phenomena involved in this process.

The small uninucleate cell enlarges very rapidly, apparently with a proportionate increase in the size of its nucleus. The elongation of the cell takes place more rapidly than the increase in its cross diameter, thus giving it a cylindrical shape. The nucleus is very distinct and exhibits a densely stained nucleole, nuclear membrane, and a less densely stained chromatic reticulum. The cytoplasm at this stage shows a very regular alveolar structure. The prophases of the first division of the nucleus become evident a little later. The chromatin becomes condensed into densely stained threads which in some cases appear to be attached to a point on the nuclear membrane from which they radiate more or less irregularly into the nuclear cavity (FIGS. 3, 6). In some cases a minute body can be faintly seen at the point of attachment of the chromatin threads on the nuclear membrane. I have been able to observe this orientation of the chromatin only in a few instances, and am in doubt whether these figures correspond entirely to those given by Harper ('05) for the asci of the higher Ascomycetes. A large oval shaped nucleole can be distinctly seen lying in the colorless nuclear sap that surrounds the chromatin strands. It is almost invariably situated near the nuclear membrane. The nucleus at this stage, though much smaller, bears a striking resemblance to the spiremes figured by Harper in the asci of *Phyllactinia* and *Erysiphe*.

Following this stage the first nuclear division occurs, which is usually in the direction of the long axis of the cell (FIG. 2). The spindle appears first as a minute streak extending across the nuclear cavity, with the chromatin and nucleole situated slightly to one side. The spindle is at first strictly intranuclear, but as it elongates the nuclear membrane disappears, and five chromosomes can be fairly accurately counted. The chromosomes are globular in shape and measure about 0.45 microns in diameter,

and yet they are distinct in well differentiated preparations. The nucleole is very distinct at this stage also and is generally situated near the center and slightly to one side of the spindle. It measures about one micron in diameter.

The first division of the nucleus has been found in relatively few cases and I have been unable to follow the later stages. The second and third divisions, however, are very easily found, and in them the process can be fairly accurately observed. The two daughter nuclei resulting from the first division are at first very small and are closely associated. They later pass to the opposite ends of the ascus, enlarge, and prepare for the second division.

The daughter nuclei in the resting stage are identical in appearance with the mother nucleus. A more or less polarized spireme is formed (FIG. 3) which is soon followed by the formation of an intranuclear spindle. Four or five chromosomes can be counted in the equatorial plate stage, and a little later nine or ten can be distinctly seen scattered along the spindle (FIG. 8). Some of these figures show densely stained strands radiating from their poles, which may be interpreted as astral rays. Centrosomes, however, cannot be distinguished with certainty in these figures. The ascus at this stage is about two-thirds mature size. The spindle elongates and becomes very narrow. Four or five chromosomes pass to each pole and the daughter nuclei are formed. The nucleole may persist on the side of the spindle during the entire process of nuclear division.

The four daughter nuclei become distributed at approximately equal distances throughout the length of the ascus. They then divide as a rule in the direction of the long axis of the cell (FIG. 9) and produce eight nuclei for the ascospores. The spindles in the third division are much smaller than in the first and second divisions and the chromosomes appear to be proportionately smaller in size. The chromosome number, however, appears to be the same throughout the three divisions.

The nuclear phenomena in the asci that arise by the direct germination of the ascospores are apparently the same as in the asci that develop from individual bud cells. This type of ascus formation is unusual, in that the upper region of the basal cell of the ascospore simply swells out into a large outgrowth, which assumes the form of a normal ascus. What causes or stimulates

the cell to make this tremendous outgrowth? Does a nucleus come in from the apical cell and fuse with that of the basal cell before this growth occurs? I am not prepared to answer these questions, but the question as to a nuclear fusion will be further discussed below.

The swollen region of the basal cell of the ascospores apparently contains a single nucleus at first (FIG. 20), which later divides in the same way as described above (FIGS. 21, 22). Here again five chromosomes can be counted in the equatorial plate stage. After division is completed, the daughter nuclei separate and undergo a second division (FIG. 24). These divisions may occur either in the direction of the long or short axis of the cell. The same thing holds for the divisions in the first type of ascus, but nuclear division is as a rule in the direction of the long axis of the ascus. The third divisions have not been observed in asci arising directly from ascospores.

The germ-tube type of ascospore germination results in the development of a mycelium in which intercalary asci are often produced. The individual cells of the hyphae develop directly into normal asci (FIG. 31) in which four to eight ascospores are produced (FIGS. 29, 30). These cells are at first apparently uni-nucleate, but as they increase in size their nuclei increase in number. Nuclear division has not been observed in these asci.

The fourth type of ascus formation follows the conjugation of two germinating ascospores. The basal cell of each of the ascospores swells and sends out a short outgrowth. These outgrowths come in contact and fuse end to end to form the conjugation canal. This conjugation results in the production of an ascus in which four or eight ascospores are formed. The apical cells and the tips of the basal cells of the two ascospores remain attached to the membrane of the mature ascus (FIGS. 32, 33).

The nuclear phenomena in this type of ascus have not been determined, but there is evidence that a nuclear fusion occurs in the tube connecting the conjugating ascospores. Each of the basal cells of the pair of ascospores contains a nucleus before conjugation occurs, whereas only one is found in the connecting tube after conjugation takes place. As the ascus develops, the number of nuclei increases to two, then to four, and finally to eight. Ascospores are then formed. Here again nuclear division figures have not been observed.

Finally, there is evidence that the asci of *Nematospora Phaseoli* may arise from the conjugation of two yeast cells. Although I have fairly good evidence of this in some of my preparations, I do not believe that it is so common as the process by which the ascus arises from a single bud cell. On the other hand, Schneider states that the asci of *N. Lycopersici* most commonly arise from a conjugation of two cells. The same type of conjugation has been described by numerous investigators as occurring among the species of *Zygosaccharomyces* and *Schizosaccharomyces*, and yet all of these investigators find that the asci in these species may also arise from individual cells.

I find stages in my preparations that suggest a conjugation of two cells, the strongest indication being a constriction that approximately divides the ascus into two equal parts. Two nuclei are present, one in each enlargement. Then in larger asci where the constriction is still apparent only one nucleus may be found. In still larger asci, two nuclei again appear. Unfortunately, however, stages appear that do not fit into the above series. Figures are found in these asci that have the appearance of nuclear fusions, but here again one must be skeptical because similar stages are found in the asci that develop from single cells, and also in those that arise directly from the germination of single ascospores. Janssens and Le Blanc described a nuclear fusion in the ascus of *S. Cerevisiae* and regarded it as a sexual fusion. Guilliermond has repeated these studies but he was unable to verify their results. He contends that there is no nuclear fusion in a yeast ascus which arises without preliminary spore or cell conjugation. My results thus far do not justify any definite statement in regard to nuclear fusion in the ascus of *N. Phaseoli*.

#### ASCOSPORE FORMATION

The ascus is practically full size at the time of the third nuclear division. It is then 70 to 80 microns long and about 10 microns in diameter. The four mitotic figures can be clearly seen lying in the faintly stained alveolar cytoplasm (FIG. 9). The final stages in these division figures and the initial stages in the formation of the ascospores have not been observed with certainty. The ascospores, however, can be distinctly seen very early in their development. They appear as small globular

bodies about 1 to 1.5 microns in diameter, and show a granular cytoplasm. They possess a definite bounding membrane that separates them from the surrounding vacuolated epiplasm. Whether this bounding membrane is formed by the fusion of astral rays as described by Harper ('05) and others in free-cell formation of ascospores in the higher Ascomycetes remains to be determined. On the other hand, there is no doubt as to the existence of an epiplasm distinct from the spore-plasm contained in the young ascospores.

The ascospores at this stage stain so densely that it is very difficult to distinguish their nuclei. The young globular ascospores now develop into the mature two-celled stage in which they are long and slender. They first assemble near the center of the ascus and then begin to elongate by sending out a pointed outgrowth that reminds one of a germ tube (FIG. 14). The four on the left elongate towards the right end of the ascus and the four on the right elongate towards the left end. A single nucleus can be distinguished in some cases when the ascospores are about one-half their mature length. As this elongation proceeds the epiplasm is more or less used up and finally the eight mature two-celled ascospores are formed, filling the entire ascus (FIG. 11). The mature ascospores are arranged in two opposite bundles of four spores each, with their whip-like appendages interlocking or more frequently curved around the opposite bundle.

The basal cell of the mature ascospore contains a single nucleus that is very easily seen, and an alveolar cytoplasm. The apical cell, as noted above, is apparently without a nucleus and its cytoplasm even at a very early stage appears to have undergone disintegration, and consists of densely stained masses (FIG. 11). It is possible that the nucleus of this cell passes into the basal cell at an early stage and fuses with its nucleus, but the evidence for this is lacking at present. I have been able to find only one case in which such an occurrence was suggested. In this case, the ascospores seemed immature but had reached the two-celled stage. The apical cells failed to show a nucleus as usual, but the basal cell of one contained two distinct nuclei. The basal cells of the others contained one nucleus as usual. I could detect no difference in the size of these nuclei.

Observations on ascospore formation in certain of the higher Ascomycetes are of interest in this connection. Faull ('04) has

found that the ascospores of several of the species of *Podospora* present a curious case of the formation of a septum in the spore without a previous division of the nucleus. The young ascospores are at first compressed and spherical but rapidly become cylindrical or rod-like. This is followed by an enlargement of the upper end in which the nucleus is to be found. The nucleus next moves down to the entrance of the small end, a septum is formed, and it passes back to the center of the upper part. The appendage develops no further, and gradually loses its cytoplasm. Brooks ('10), studying ascospore formation in *Gnomonia erythrostoma*, found that after the spore membrane has been laid down the nucleus undergoes division towards the base of the ascospore. One of the two daughter nuclei thus formed passes to the extremity of the spore, and a septum is laid down between the two nuclei, cutting the ascospore into cells of unequal size. The nucleus of this tail-cell gradually disorganizes. He found also in germinating the ascospores, that only the larger cells send out germ tubes.

It should be noted, however, in this connection that the sterile cells in the ascospores of these fungi are much smaller than the functional cells; whereas in *N. Phaseoli* the apparently functionless cell is equal in size to the functional cell.

#### DISCUSSION

My cytological studies have shown that the ascus of *Nematospora* is typical in respect to the differentiation of spore-plasm and epiplasm. The ascus is uninucleate at a rather young stage, and this single nucleus undergoes the regular triple division characteristic of practically all asci. Eight ascospores are regularly formed, though I have observed a few cases in old cultures where a smaller number was formed. It could be clearly seen in these cases that the reduced number was due to the abortion of some of the young spores, as in the case of the mildews such as *Phyllactinia* and *Erysiphe*.

The ascospores are unquestionably formed by free cell formation: that is, they are cut out of the ascus as globular cells surrounded by the epiplasm which is later more or less used up in their development to mature size. The figures, however, are too minute to permit one to follow the exact details of the process of spore delimitation. I have also so far failed to settle the

further point as to the existence of a nuclear fusion in the young ascus.

There seems no adequate reason for regarding *Nematospora* as a "doubtful Ascomycete," so far as its ascus is concerned. As noted earlier, Guilliermond ('12) puts *Nematospora*, *Monospora*, and *Coccidiascus* together as his fifth group of *Saccharomycetes*, and designates them as budding yeasts with uncertain affinities. As recognized by Guilliermond, the relationship of this group to the other groups is by no means clear. Guilliermond's series consists of the following groups: (1) Yeasts multiplying by partition; asci usually derived from a conjugation. (2) Budding yeasts; asci usually derived from a conjugation. (3) Budding yeasts which form a slimy scum in sugar solutions; ascospores round or oval in shape. (4) Budding yeasts which generally produce ether; ascospores characteristically hat-shaped. (5) Yeasts in which the relationships are not well known.

In my opinion *Nematospora* has a typical ascus, and at the same time is unquestionably a member of the yeast series. The evidence of the relationship of the whole series to the Ascomycetes is thus strengthened. Whether *Nematospora* is to be regarded as a primitive or degenerate type is a more difficult question. The whole group with its interesting relations to the insects and incipient parasitic habits on green plants appears to be excellent material for the study of the general problems as to the origin and relationship of the entire yeast series.

The genus *Nematospora* is apparently closely related to the genera *Monospora* and *Coccidiascus* which it resembles morphologically, especially in the shape of the ascospores and in the production of budding yeast-like cells. *Monospora* differs from the others in having a single ascospore. This genus should be studied cytologically to determine whether there is a triple nuclear division in the ascus. These three genera in my opinion constitute a phylogenetic unit.

The genera *Eremothecium* Borzi, and *Protascus* Dangeard, somewhat resemble *Nematospora* in respect to the shape and arrangement of their spores. *Eremothecium* has about 50 spores formed in its fruiting body and there is no evidence that they are formed by free cell formation. *Protascus*, on the other hand, has only 32 spores, and Dangeard has presented evidence that shows that they are formed by free cell formation. Asci

with more than eight spores are of course well known, for example, *Rhyparobius*, *Podospora*, *Thecotheus*, etc. But whether the asci of *Eremothecium* and *Protascus* belong to this class must be determined by further cytological study. The further point as to whether the resemblance of *Eremothecium* and *Protascus* should be regarded as merely accidental or as an indication of relationship remains unsettled as yet.

The species of the genera *Nematospora*, *Monospora* and *Coccidiascus* are all parasites. *Monospora bicuspidata* is parasitic on *Daphnia*, *Coccidiascus Legeri* is parasitic on *Drosophila funebris*, and the five species of *Nematospora* are parasitic on the fruits of a wide range of plant families. *Nematospora species C* and *D*, Nowell, are parasitic on the fruits of the following plants in the British West Indies; tomato, Lima bean, sword bean, castor oil bean, cowpea, cotton, coolie pepper, sweet orange, *Asclepias* sp., *Jatropha* sp., *Cassia* sp., *Indigofera* sp., *Tephrosia* sp., *Crotalaria* sp., and *Dolichos Lablab*. Infection, according to Nowell, is brought about by the punctures of the cotton stainer (*Dysdercus delauneyi*), the green bug (*Nezara viridula*), the leaf-footed tomato bug (*Leptoglossus balteatus*), and the red tomato bug (*Phthia picta*).

*Nematospora Coryli* is parasitic on hazel nuts, *N. Lycopersici* is parasitic on tomato fruits, and *N. Phaseoli* is parasitic on Lima beans, Bird-eye beans, and Black-eye cowpeas. Infection with *N. Phaseoli*, as I have shown, takes place in the punctures made by the green bug (*Nezara hiliaris*). We have then two genera of the group, *Monospora* and *Coccidiascus*, passing their whole life history as parasites in respectively a crustacean and a fly, *Daphnia* and *Drosophila*, while the third genus, *Nematospora*, with its much larger number of species, passes its complete cycle of development, so far as yet known, as a parasite in some one of the wide range of host plants just enumerated, but again, so far as known, depends entirely on insects, such as *Dysdercus delauneyi*, *Nezara viridula*, *Nezara hiliaris*, *Leptoglossus balteatus* and *Phthia picta*, for gaining access to its hosts. The situation is most interesting from the standpoint of the whole question of insect carriers of pathogenic organisms.

The method of infection of *Drosophila* is unknown, though, as Chatton notes, the flies feed on mother of vinegar. Metchnikoff does not state the method of infection in *Daphnia*, but he reports



large quantities of vegetative cells, asci and ascospores in the tissues of the sick and dead *Daphnia*. He also reports the presence of free ascospores in the intestinal tract of the healthy *Daphnia*. This naturally suggests that the ascospores are taken into the intestinal tract by the feeding of *Daphnia* in contaminated water.

The question whether *Nezara hilaris* is also a host for *Nematospora Phaseoli*, and may possibly carry it through the winter is a matter of obvious importance. Infection with *Nematospora Coryli* and *N. Lycopersici* has not been reported as due to insect punctures, but this is probably due to the fact that the insect punctures were overlooked. The type of lesions produced on the cotyledons of the hazel nuts and on the tomato fruits strongly suggest their origin in insect punctures.

The fact that these yeasts parasitic on seed plants are so largely, if not exclusively, carried by insects, together with the fact that the other species of the group, *Monospora bicuspidata* and *Coccidiascus Legeri*, are themselves parasitic respectively on crustaceans and insects, presents, as noted above, an interesting situation bearing on the general problems of alternate hosts and insect carriers. The ordinary food substrata of yeasts are fruit juices capable of fermentation; and these juices are also a common food for insects, especially flies like *Drosophila*, the host of *Coccidiascus Legeri*. The situation seems naturally to suggest that yeasts now parasitic on green plants and carried by puncturing insects may have been derived from yeasts parasitic on insects, which in turn were derived from yeasts which live normally in fermenting fruit juices. Further data as to the possibility that the parasitic *Nematosporas* may multiply and perhaps pass the winter in *Nezara* is very much needed.

The asci of *Nematospora Phaseoli* may arise from individual yeast cells, from direct germination of the ascospores, from a conjugation of two ascospores, from single cells in the mycelial strands, and perhaps from the conjugation of two yeast cells. All of these cases are paralleled among the genera of the *Saccharomycetes*. The asci of the species of *Schizosaccharomyces* and *Zygosaccharomyces* most commonly arise from the conjugation of two bud cells, yet the individual cells often develop into asci without conjugating. In *Saccharomyces Ludwigii*, *Willia Saturnus* and yeast *Johannisberg II*, the asci usually develop

from single bud cells and the ascospores conjugate two by two at the time of germination. Budding from the zygosporangium thus formed usually follows, but it is not uncommon for asci to develop directly from a germ tube which arises from the conjugated pair. The single ascospores may also develop directly into asci. The asci of *Saccharomyces Cerevisiae* develop from single cells as a rule but, according to Hansen, they may also develop from the conjugation of two ascospores or the single ascospores may germinate directly into asci. In addition to the above methods of forming asci, *Saccharomyces Ludwigii*, *Pichia membranaefaciens*, and the yeast from pulque often form a mycelium on the surface of old cultures in which each cell of the hyphae may develop into an ascus with the normal number of ascospores.

Parallel cases are also to be found among the Endomycetaceae. In *Endomyces capsularis*, the asci are formed from single cells in the mycelium, but in some cases the ascospores form a bud or a germination tube that develops directly into an ascus. The asci of *Endomyces javanensis* develop from the individual yeast cells or from single cells in the mycelium. The asci of *Eremascus fertilis*, *Endomyces fibuliger*, and *Endomyces Magnusii* commonly develop from a conjugation of two cells in the mycelium, but they may also develop from single cells without conjugating.

It is obvious from all this diversity in the method of ascus formation in the various groups that, in so far as the process is associated with sexuality, modified and parthenogenetic conditions are suggested. The material is certainly very favorable for the study of the effects of environmental conditions on the occurrence and the significance in the life cycle of sexual cell fusions.

The data here presented are also of fundamental significance in connection with our conceptions of alternation of generations in both the lower fungi and the algae. The Nematosporas are relatively so favorable for cytological study that they constitute especially good material for the study of all these problems.

#### SUMMARY

1. *Nematospora* is parasitic on a wide range of plants, but the Leguminosae predominate in the list.
2. Infection is associated with the punctures of particular insects.

3. The vegetative phase of *Nematospora* is typically yeast-like as a rule, but when grown in tap water, distilled water, or a very dilute solution of beer wort, a rudimentary mycelium is produced. A rudimentary mycelium is also produced around the borders of old colonies on solid media.

4. In the method of formation of its ascus *Nematospora* is in conformity with typical Ascomycetes in respect to the differentiation of spore-plasm and epiplasm, the triple division of the primary ascus nucleus, and the number of ascospores formed. The spores are formed by free cell formation.

5. The nuclear divisions in the ascus are typically mitotic. A spindle is formed and four or five chromosomes can be distinguished in the equatorial plate stage of the first and second divisions. The same number apparently holds for the third division, but the minuteness of the figures makes this a difficult matter to determine with certainty.

6. *Nematospora* is apparently rather closely related to the genera *Monospora* and *Coccidiascus*, which it resembles morphologically, so that these genera appear to form a natural group under Saccharomycetes.

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#### Explanation of plates 7-9

All figures were drawn with a camera lucida and a Leitz ocular no. 4; FIGS. 1, 3, 5, 10, 12-18b, 20-24 with a Leitz 1/16 in. oil imm. objective, N. Ap. 1.32; FIGS. 2, 4, 6, 7, 8, 9, 11, 19, 22 with a Leitz 1/12 in. oil imm. objective, N. Ap. 1.30; FIGS. 25-33 with Leitz objective no. 6, N. Ap. 0.82. The magnification is given with each figure.

#### Plate 7

FIG. 1. Young ascus with a single nucleus.  $\times 2042$ .

FIG. 2. Primary nucleus of the ascus; equatorial-plate stage, five chromosomes and a nucleole.  $\times 1600$ .

FIG. 3. Part of a binucleate ascus, showing the chromatin strands radiating from a point on the nuclear membrane and a nucleole lying in the nuclear space.  $\times 2042$ .

FIG. 4. A young uninucleate ascus.  $\times 1600$ .

FIG. 5. Portion of a 4-nucleate ascus, showing two of the mitotic figures with five chromosomes.  $\times 2042$

FIG. 6. Uninucleate ascus with the nucleus in the spireme stage.  $\times 1600$ .

FIG. 7. Ascus with the eight young ascospores.  $\times 1737$ .

FIG. 8. Binucleate ascus with the nuclei in the metaphase stage; nine chromosomes can be distinguished.  $\times 1600$ .

FIG. 9. Ascus with four mitotic figures; four or five chromosomes and a nucleole can be distinguished in each figure.  $\times 1600$ .

FIG. 10. Ascus with two mitotic figures; five chromosomes and a nucleole can be distinguished in each of these figures.  $\times 1874$ .

FIG. 11. Mature ascus, showing the eight mature ascospores; the basal



cell of each ascospore contains a single nucleus, while the apical cell contains only masses of disintegration products.  $\times 1737$ .

### Plate 8

FIG. 12. Ascospore with three nuclei in the swollen upper region of the basal cell; the original nucleus of this cell apparently divided, giving two, and then one of these underwent a second division, resulting in the two smaller ones.  $\times 2042$ .

FIG. 13. Germinating ascospore. Budding is taking place from the upper region of the basal cell; the upper cell contains masses of disintegration products.  $\times 2042$ .

FIG. 14. Ascus with the eight young ascospores, two of which have begun to elongate.  $\times 1737$ .

FIGS. 15a, 15b, 16. Ascospores germinating by the budding process.  $\times 2042$ .

FIG. 17. Ascospore showing the swelling of the upper region of the basal cell preparatory to germination.  $\times 1894$ .

FIGS. 18a, 18b. Mature ascospores.  $\times 1874$ .

FIG. 19. Uninucleate bud cells.  $\times 1082$ .

FIG. 20. Basal cell of an ascospore germinating directly into an ascus.  $\times 2042$ .

FIG. 21. Same as 20, with the nucleus in the process of division.  $\times 2042$ .

FIG. 22. Ascus formed by direct germination of the basal cell of the ascospore. The primary nucleus is undergoing division, and five chromosomes and a nucleole can be distinguished on the spindle. Note the contents of the apical cell.  $\times 1600$ .

FIG. 23. Binucleate ascus formed by direct germination of the ascospore.  $\times 2042$ .

FIG. 24. Second nuclear division in an ascus formed by direct germination of the basal cell of an ascospore.  $\times 2042$ .

### Plate 9

FIGS. 25, 26. Asci formed on the tips of mycelial strands.  $\times 500$ .

FIG. 27. Intercalary asci before ascospores are formed.  $\times 312$ .

FIG. 28. Intercalary asci.  $\times 500$ .

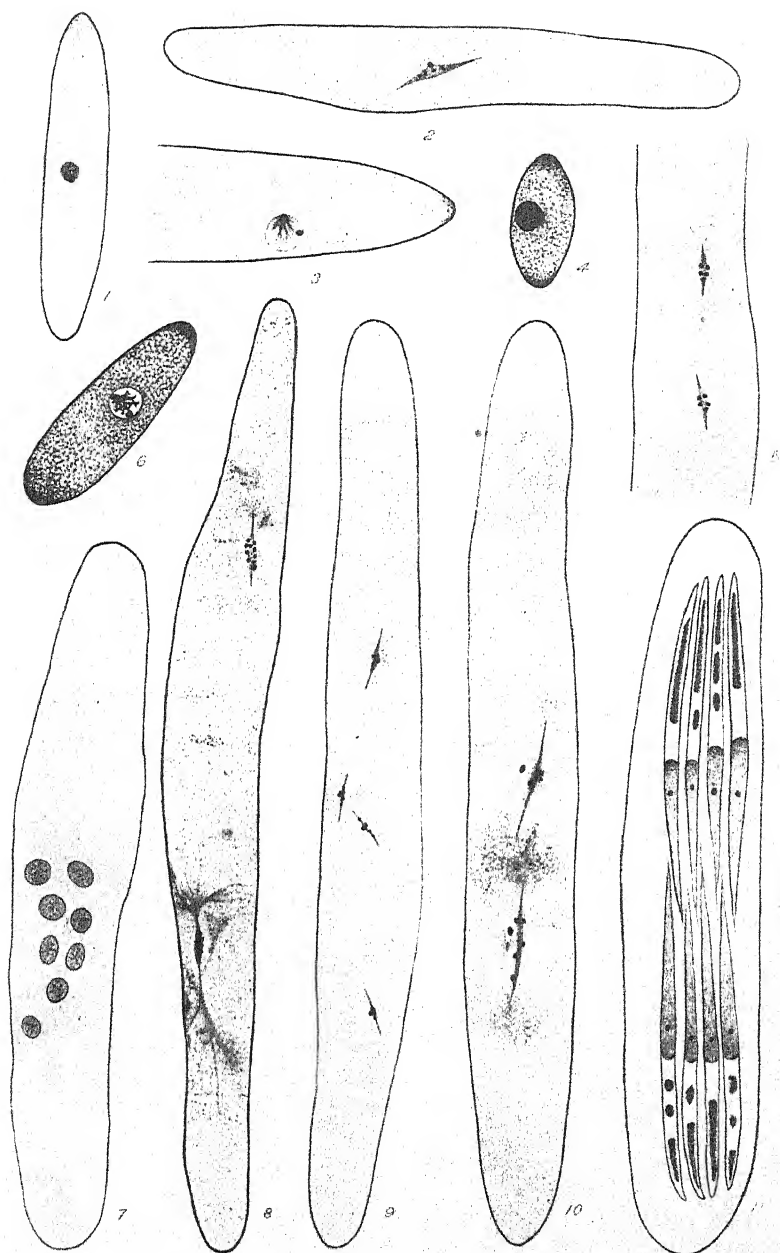
FIG. 29. Intercalary ascus with ascospores.  $\times 312$ .

FIG. 30. Intercalary asci, one with ascospores.  $\times 500$ .

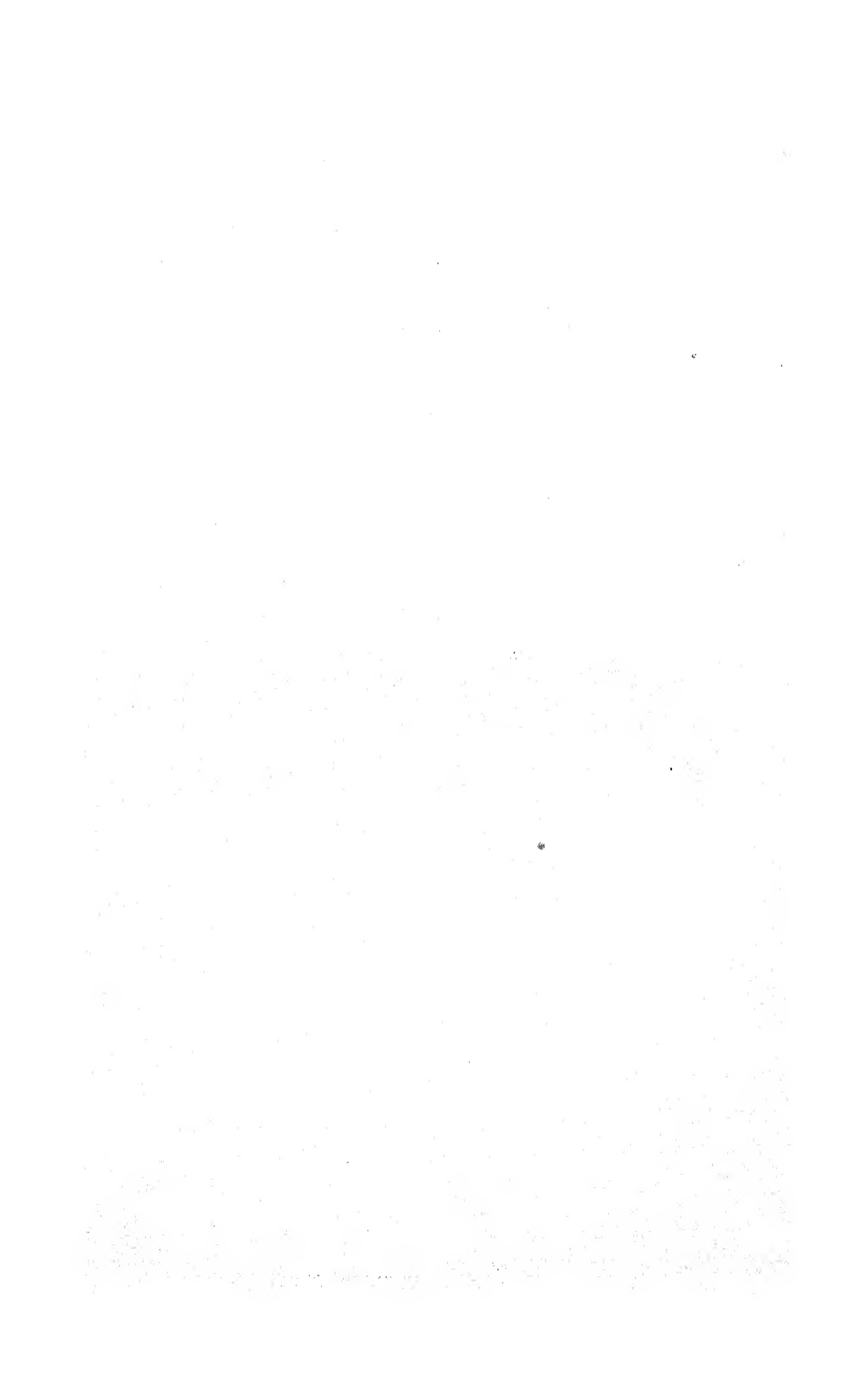
FIG. 31. Germinating ascospore, showing the formation of intercalary asci.  $\times 624$ .

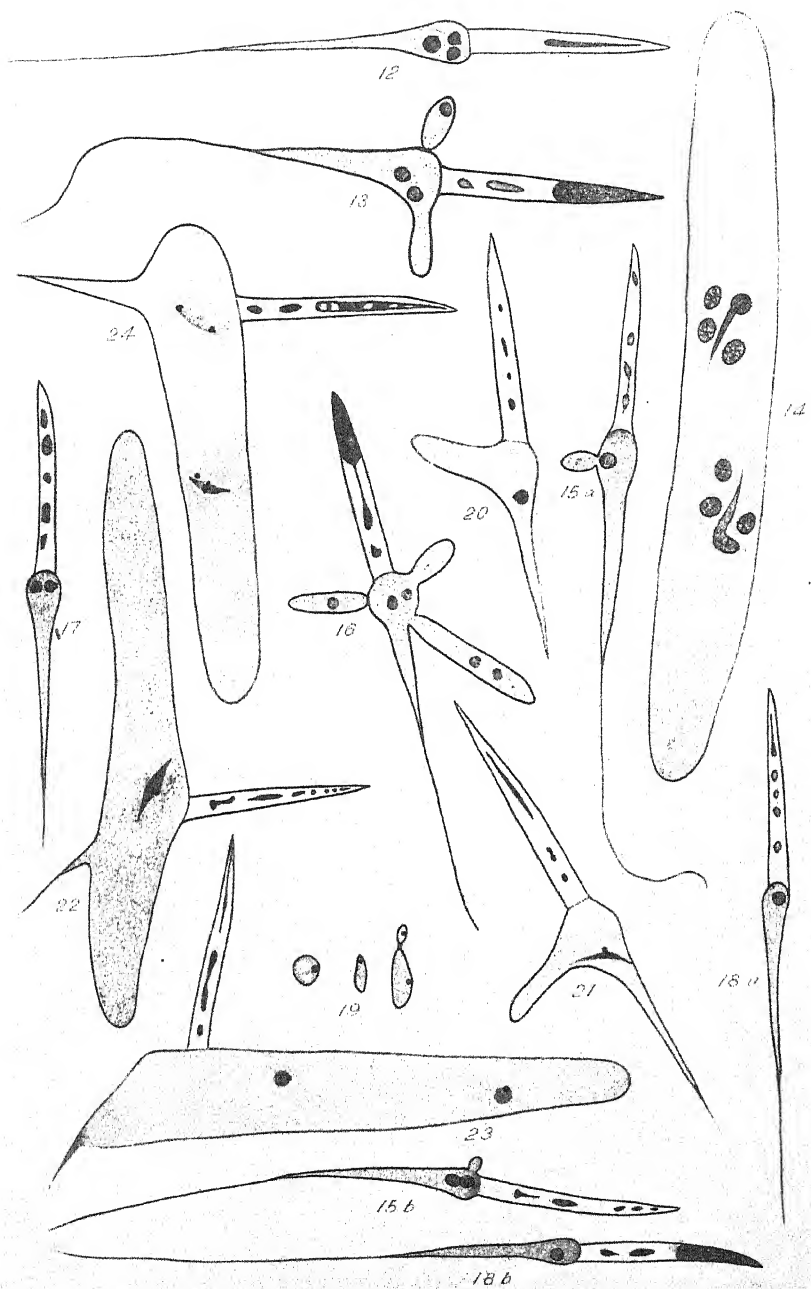
FIG. 32. Two ascospores conjugating to form an ascus.  $\times 500$ .

FIG. 33. An ascus formed by the conjugation of two ascospores.  $\times 500$ .



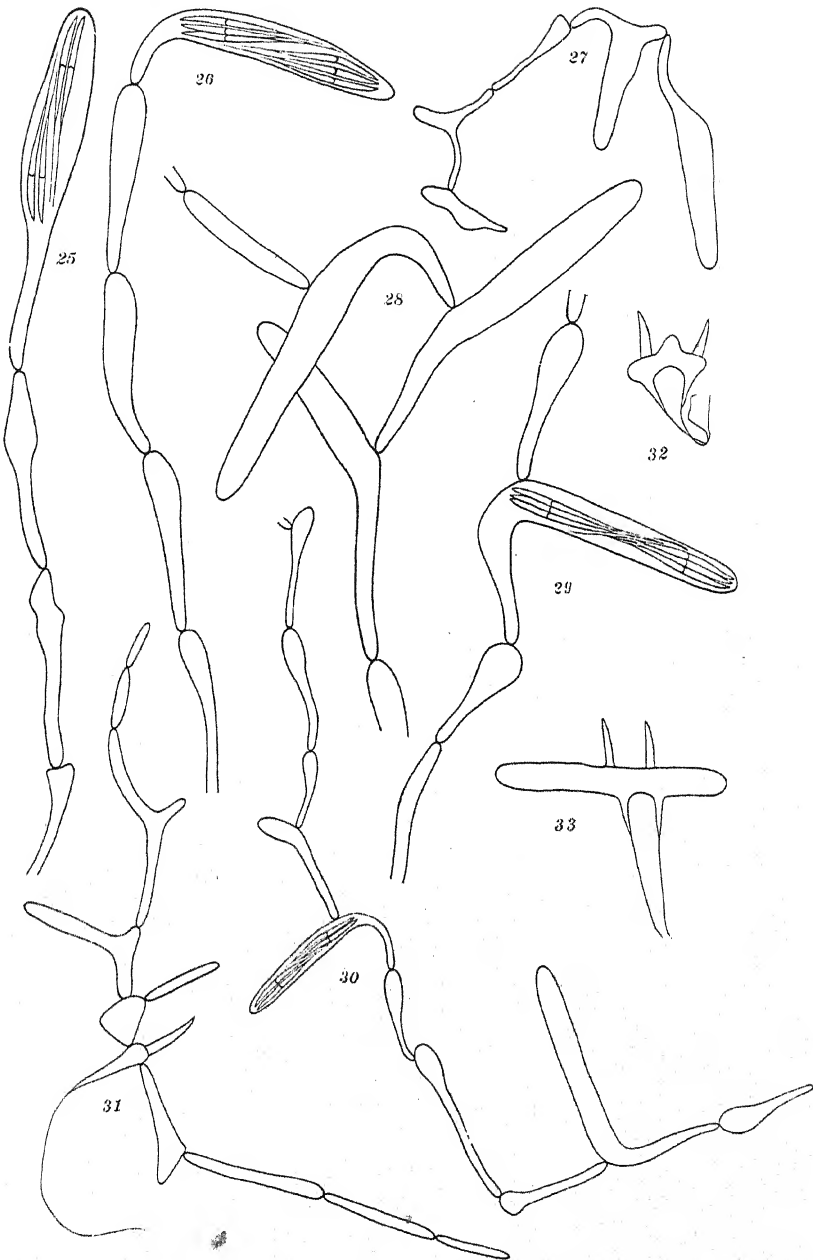
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## Growth stimulation of *Aspergillus niger* by a vitamine B preparation\*

NELLY JACOB SCHELLING

(WITH FOURTEEN TEXT-FIGURES)

The rôle of vitamines as accessory food substances in the nutrition of animals has become so important a question that it seems well to have more information upon their influence on the growth of plants. As will be seen from the brief survey of the literature which is given here our knowledge of the relation of vitamines and plants is rather meager. Of the published work, that of Lepeschkin (18) referred to later, most nearly coincides with the present account, though it by no means duplicates it. Lepeschkin's paper appeared, as will be seen by the date, at about the time that this study was completed.

It was the purpose of the present work to determine in how far the effects of a preparation of water soluble vitamine B from yeast upon the growth of *Aspergillus niger* are comparable to those obtained by stimulation with minute doses of chemical poisons. A few observations were also made on the effect of the same vitamine preparation upon wheat seedlings and upon *Lemna*.

Wildiers (30) in 1901 stated that he had found it impossible to obtain normal growth of *Saccharomyces Cerevisiae* in a synthetic inorganic medium if very small inoculations were made. Heavy inoculations resulted in abundant, normal growth of the organism. This at once gave Wildiers the clue to the unexplained discrepancies between the results of Liebig's and Pasteur's experiments on yeast, grown in mineral salt solutions. Biologists at the time took little notice of Wildiers' paper. The question did not become one of vital interest until Funk and other investigators discovered yeast to be a rich source of vitamine B. Most workers today hold that the *Saccharomycetes* require vitamines for their normal metabolism.

During the last few years a considerable amount of work has been done on the necessity of vitamines for the development of certain pathogens, especially *Bacillus Influenzae* (Pfeiffer's bacillus). According to Thjötta (28), Thjötta & Avery (29), and

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\* Contributions from the Department of Botany of Columbia University, no. 340.



Davis (8, 9) two growth accessory factors are involved in the growth of *B. Influenzae*. The two substances were found to differ in their thermostability (Davis 8, 9). Both are reported to be contained in the blood corpuscles. Davis (7) tested the effects of vitamins from different sources on *B. Coli*, *B. typhosus*, *B. prodigiosus*, and *B. Diphtheriae*. In no case particular stimulation was observed.

What little work has been done on the vitamins in relation to the fungi leaves us pretty much in the dark as to their rôle and importance in these forms. Linossier (19) found *Oidium lactis* under certain conditions favorably influenced by the addition of vitamins to the nutrient solution. According to his observations, the fungus, if in very vigorous condition, can live perfectly normally on inorganic nutrients alone. Either it does not need vitamins for its growth, or it is capable of synthesizing them. If the vitality of the organism is in any way reduced (as by heat, age, etc.) the addition of growth promoting substances to the nutrient solution proved to have marked effects. Linossier furthermore observed that vitamins are absolutely essential to the growth of *Oidium lactis* if very small inoculations are made. Without vitamins in the solution, the fungus was found to germinate slowly and with difficulty. After about six days the controls caught up with the stimulated cultures.

Lepeschkin (18) confirmed Linossier's observation that the effect of vitamins upon fungi is evident during the first few days only. Working with *Aspergillus niger* and *Penicillium glaucum*, he noted very marked effects of the growth promoting substances during the early stages of germination, while there was practically no difference between the individual cultures after several days.

Lumière (20) denied any influence of the vitamins upon the growth of fungi. The "stimulation" observed after the addition of vitamins is attributed by this investigator not to the growth accessory substances as such, but to the addition of salts to poor synthetic media. The experiments which led Lumière to make such statements must be said to be inconclusive.

Goy (16) working with *Saccharomyces Cerevisiae*, *Mucor Mucedo*, *Aspergillus niger*, *Penicillium glaucum*, and *Bacillus Megatherium*, found these organisms to develop normally in mineral salt solutions. Much more proliferation was obtained

upon addition of small amounts of the medium in which previously had been grown either the same or a different species. The paper, unfortunately, leaves us in the dark as to the exact amount of old medium added, so that an interpretation of Goy's results is rather difficult. If minute quantities were used, the stimulation of proliferation suggests that from the organisms in question certain growth stimulating substances diffuse out into the medium. If, on the other hand, larger quantities of the old medium were added, the question of increased food supply might come into play.

Willaman (31) published a paper in 1919 on the function of vitamins in the metabolism of *Sclerotinia cinerea*, the brown rot fungus of plums and peaches. The organism did not develop unless vitamins from some source or other were added to the medium, a solution of mineral salts with the addition of asparagine and sucrose. Willaman found the amount of vegetative growth not in proportion to the juice added, large amounts of the latter causing slight inhibition of growth in the majority of cases. A large number of vitamin extracts which were examined, were found to stimulate the vegetative growth of *Sclerotinia*, but only very few induced reproduction. Furthermore, Willaman found the amount of sporulation not necessarily proportional to the amount of vegetative growth. These observations suggested the possibility of two different vitamins at work, one stimulating vegetative growth, the other one important in reproduction. Willaman, however, believes that a single vitamin is responsible for the stimulation of both vegetative growth and reproduction of *Sclerotinia cinerea*.

Bottomley (1-4) developed the theory that not only lower forms, but also green plants require growth promoting substances or auximones. He found that *Lemna minor* and several other aquatics did not develop normally in mineral salt solutions without the addition of auximones. These organic growth promoting substances were obtained from soil, as a result of the bacterial decomposition of peat, from cultures of *Azotobacter Chroococcum*, and *Bacillus radicicola*, as well as from manure (Mockeridge 21). The identity of the auximones with vitamins is indicated by the fact that the phosphotungstic acid, and the silver fraction precipitate both substances from solutions. Auximones were found to have a marked stimulating effect

upon the rate of reproduction of *Lemna minor*. Cytological examination of stimulated plantlets showed larger nuclei, denser cytoplasm, and fewer, smaller air-spaces than the controls. Bottomley obtained analogous effects of auximones on wheat but these plants did not give as satisfactory results as *Lemna minor*. This is due to the fact that wheat, by virtue of having an endosperm, is not as dependent upon the medium. Furthermore, it has been proved conclusively that the dry wheat grain contains a small quantity of vitamins, while the germinating grains are very rich in these substances.

Rosenheim (25) tested the effects of auximones on the growth of *Primula malacoides*. After a treatment of three weeks the plants were found to have larger and darker leaves, as well as a greater abundance of flowers than the controls.

#### EXPERIMENTAL PART

The methods used were those that have been employed by many previous investigators and are consequently described but briefly here. The source of the vitamin used was the preparation known as Vitamin B Harris. Pyrex glassware was used in all cases for the culture dishes, as giving a glass with minimum solubility, and the water employed was distilled twice over a block tin coil. Conductivity tests showed that this water was of high degree of purity. The chemicals employed were those of Merck and Co., Reagent grade, and as a sugar source Pfanstiehl's sucrose was used.

Except in one case, mentioned later, the culture flasks used were of 150 cc. capacity and of the Erlenmeyer form. Fifty cubic centimeters of culture solution were used to each flask. This solution was made up by the formula of Pfeffer which has been largely employed for similar work. Its composition is as follows:—

$\text{KH}_2\text{PO}_4$	0.5 gram
$\text{MgSO}_4$	0.25 "
$\text{NH}_4\text{NO}_3$	1.0 "
$\text{Fe}_2\text{SO}_4$	trace
Sucrose	5.0 "
Water	100 cc.

The yeast vitamin solution was added from a standard solution made up fresh for each set of cultures. Two hundred milligrams

of the vitamine powder were weighed out and dissolved in four cc. of water. By means of a pipette delivering a drop of as nearly as possible one twentieth of a cubic centimeter volume, certain definite quantities were added as follows:—

	Vit. sol. added	Equivalent of	%	H <sub>2</sub> O added
Culture A	(Control) 0			16 drops
" B	1 drop	2.5 mg. dry vit.	.05	15 "
" C	2 drops	5.0 " " "	.10	14 "
" D	4 "	10.0 " " "	.20	12 "
" E	10 "	25.0 " " "	.50	6 "
" F	16 "	40.0 " " "	.80	0 "

The water was added to keep the surface areas and concentrations of nutrients equal in all cases. The cultures were then inoculated with the *Aspergillus niger* spores, and placed in the incubator, the temperature of which was kept at 35° C. After three and a half days the mycelium felts were filtered off on weighed filter paper, washed with distilled water, and dried for forty-eight hours in a hot air drying oven at about 70° C.

Vitamine B was found to be a stimulant to both vegetative growth and reproduction of *Aspergillus niger*. TABLE I shows the stimulation of growth, measured by the increase in the dry weight of the mycelial felts.

TABLE I. DRY WEIGHTS OF STIMULATED ASPERGILLUS CULTURES

	Control	2.5 mg.	5 mg.	10 mg.	25 mg.	40 mg.
	.482 gr.	.491 gr.	.475 gr.	.603 gr.	.621 gr.	.713 gr.
	.289	.394	.399	.490	.452	.631
	.424	.487	.492	.405	.463	.554
	.408	.471	.344	.436	.445	.406
	.344	.410	.425	.508	.491	.452
	.394	.371	.408	.584	.584	.608
	.345	.417	.386	.526	.676	.689
	.380	.320	.399	.398	.442	.488
	.398	.396	.402	.510	.483	.593
	.366	.415	.367	.426	.512	.582
	.357	.441	.388	.567	.567	.579
	.355	.387	.399	.437	.538	.519
	.419	.452	.438	.454	.572	.565
	.393	.404	.437	.442	.503	.625
Average dry weight	.382 mg.	.418 mg.	.411 mg.	.484 mg.	.524 mg.	.571 mg.
Average increase over Control		9.4%	7.5%	26.7%	37.1%	49.4%

The results expressed in this table show at once some very striking differences as compared with those obtained by stimulation with minute quantities of toxic substances, such as zinc sulphate. In the case of the vitamine cultures the increase in dry weight is very gradual. In a typical zinc stimulated culture, on the other hand, the smallest dose of the salt used produces a very marked increase in weight which is comparatively little less than the maximum yield.

High concentrations of vitamines affect the organisms in one of three ways, as reported in the literature:

(1) For certain organisms, for instance the yeasts, there is an optimum concentration of the vitamine, beyond which point the curve drops (Euler & Myrbäck 10, Funk & Freedman 15).

(2) Only a definite amount of vitamine is available to the organism; higher concentrations have no effect. Thus, Lepeschkin (18) states that yeast requires only a very small amount of vitamines, which quantity it was found needless to increase.

(3) Chick & Hume (5) apparently do not believe in a maximum concentration of vitamines. They found birds to be in a "remarkably fine condition," if fed on polished rice, and an excess of vitamines.

Graphic representation of the results of the stimulation of growth of *Aspergillus niger* by vitamine B shows a smoothly ascending line, thus suggesting a reaction of type 3 (see FIG. 1).

A reaction of type 1 could not be induced, even if exceedingly high concentrations of vitamines were used. A series of experiments was carried out to establish this point. Vitamine powder was added to the culture medium minus the ammonium nitrate. The results are summarized in TABLE 2.

TABLE 2. DRY WEIGHTS OF THE CULTURES MINUS  $\text{NH}_4\text{NO}_3$

	50 mg.	100 mg.	125 mg.	200 mg.	250 mg.	500 mg.
		.477 gr.		.604 gr.	.685 gr.	.900 gr.
	.300 gr.	.458		.545	.618	
					.635	.950
					.690	.958
			.554 gr.		.791	.898
			.500		.728	.996
			.596		.846	1.276
			.585		.699	1.097
Average	.300 gr.	.467 gr.	.558 gr.	.574 gr.	.711 gr.	1.010 gr.

Conidia formation in the case of the 125 mg. vitamine powder culture occurred much earlier than in the case of the control. As the vitamine supply was doubled and quadrupled, sporulation was retarded. Even when the supply of vitamine powder was as high as 500 mg. conidia were formed at an earlier stage than in the controls without vitamine.

The above experiments not only prove that high concentrations of vitamins do not inhibit growth and reproduction of *Aspergillus niger*, but they also show that vitamine B is an excellent nitrogen source for the fungus.

Several sets of experiments were carried out in order to determine whether the degree of stimulation would show any variation if the cultures were grown for different lengths of time.

TABLE 3. PERIOD OF GROWTH: FORTY HOURS\*

	Control	10 mg. Vit./50 cc.	40 mg. Vit./50 cc.
	.455 gr.	.515 gr.	.603 gr.
	.448 "	.505 "	.577 "
Average	.451 gr.	.510 gr.	.590 gr.

TABLE 4. PERIOD OF GROWTH: TWELVE DAYS

Control	2.5 mg. Vit./50 cc.	5 mg.	10 mg.	40 mg.
.532 gr.	.611 gr.	.542 gr.	.632 gr.	.698 gr.

Graphic representation of the results expressed in TABLES 1, 3 and 4 shows three gradually rising lines which run more or less parallel to one another (FIG. 1).

The results expressed in TABLE 4 are not in accord with those obtained by Lepeschkin (18), and Linossier (19). The former states that the effects of vitamins on *Penicillium glaucum* and on yeast are noticeable only during the first few days, when the organism has an excess of food, while after several days no difference between the individual cultures was noted. Linossier found the same thing to hold true for *Oidium lactis*.

Considerable differences were noted between the microscopic appearance of vitamine and zinc cultures. The mycelium of the latter is leathery, knotted, and thrown into heavy folds. The mycelial felts in the case of the vitamine cultures are practically

\* In order to have as large a surface area as possible, 250 cc. Erlenmeyer flasks were used for this particular experiment.

smooth, very thick and tenuous. Vitamine B accelerates the formation of conidia, while stimulants in the form of toxic substances retard or suppress sporulation. The addition of small quantities of tomato juice to the medium was found to have exactly the same effect on the time of fructification as the addition of yeast vitamine. It appears that in the case of *Aspergillus niger* early conidia formation is one of the main reactions caused by vitamins.

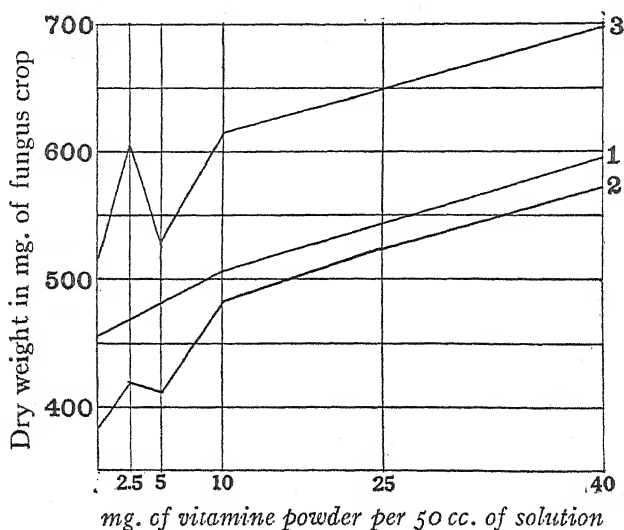


FIG. 1. 1, growth in forty hours; 2, growth in three and one-half days; 3, growth in twelve days.

To study the stimulation of the fungus during its early stages of growth, the percentage of germinating spores within a given time had to be determined. Hanging drop cultures in the usual Van Tieghem cells were used for this purpose and the culture solutions prepared as for the flasks. As few spores as possible were inoculated into the hanging drop. The cultures were grown in an incubator at 35° C. The results expressed in TABLES 5 and 6 suggest that the maximum reaction of vitamins on *Aspergillus niger* occurs within the first five hours after inoculation.

In another series of experiments vitamine powder was added to double distilled water, instead of to the culture solution. Analogous results to those expressed in TABLES 5 and 6 were obtained, and are set forth in TABLES 7-9.

TABLE 5. PERCENTAGE OF GERMINATING SPORES, FIVE HOURS AFTER INOCULATION IN NUTRIENT SOLUTION + VITAMINE:

	<i>Control</i>	<i>2.5 mg.</i>	<i>5 mg.</i>	<i>10 mg.</i>	<i>25 mg.</i>	<i>40 mg.</i>
	52.1	72.4	72.0	79.0	82.7	81.3
	56.3	66.6	71.1	78.2	84.3	84.1
	65.3	70.7	73.8	77.8	90.1	93.2
	64.4	76.4	84.6	86.0	91.2	91.4
	44.2	83.6	81.2	82.7	89.0	90.2
	52.9	75.6	81.5	82.3	81.3	88.1
Average	55.8	74.2	77.3	81.0	86.4	88.05

TABLE 6. PERCENTAGE OF GERMINATING SPORES, NINE HOURS AFTER INOCULATION IN NUTRIENT SOLUTION + VITAMINE:

	<i>Control</i>	<i>2.5 mg.</i>	<i>5 mg.</i>	<i>10 mg.</i>	<i>25 mg.</i>	<i>40 mg.</i>
	95.9	97.8	96.1	96.0	97.9	98.9
	82.3	92.8	94.2	92.9	97.9	97.0
	83.1	92.7	92.2	94.0	96.8	97.0
Average	87.1	94.4	94.19	94.3	97.5	97.3

TABLE 7. PERCENTAGE OF GERMINATING SPORES, FIVE HOURS AFTER INOCULATION IN DISTILLED WATER + VITAMINE:

	<i>Control</i>	<i>2.5 mg.</i>	<i>10 mg.</i>	<i>25 mg.</i>	<i>40 mg.</i>
	9.1	34.8	50.6	59.9	65.7
	7.2	25.5	45.3	50.3	67.0
	10.1	25.2	44.0	53.3	62.1
Average	8.8	28.5	46.6	54.5	64.9

TABLE 8. PERCENTAGE OF GERMINATING SPORES, TEN HOURS AFTER INOCULATION IN DISTILLED WATER + VITAMINE:

	<i>Control</i>	<i>2.5 mg.</i>	<i>10 mg.</i>	<i>25 mg.</i>	<i>40 mg.</i>
	17.6	44.0	55.4	61.8	83.3

TABLE 9. PERCENTAGE OF GERMINATING SPORES, TWENTY-FOUR HOURS AFTER INOCULATION IN DISTILLED WATER + VITAMINE:

	<i>Control</i>	<i>2.5 mg.</i>	<i>10 mg.</i>	<i>25 mg.</i>	<i>40 mg.</i>
	28.1	68.6	72.2	80.3	93.5
	25.9	67.7	73.4	81.9	88.7
Average	27.0	68.1	72.8	81.1	91.1



The results set forth in TABLES 5-9 are summarized graphically in FIG. 2.

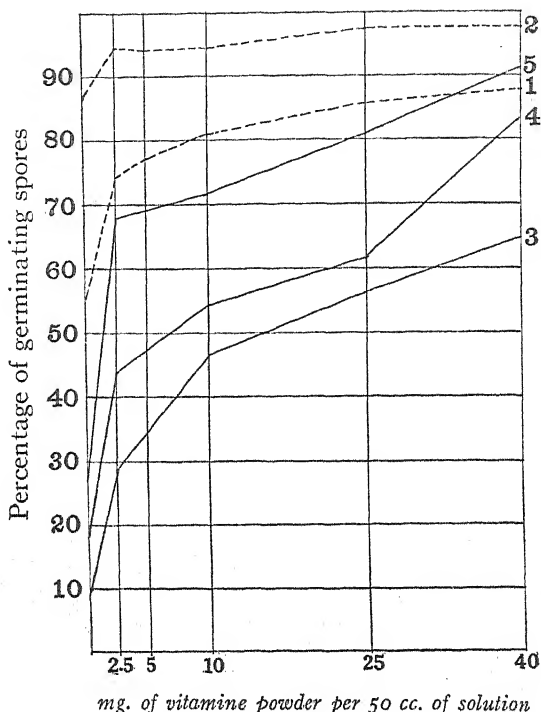


FIG. 2. 1 and 2 in nutrient solution + vitamin, after five and nine hours respectively. 3, 4 and 5 in distilled water + vitamin, after five, ten, and 24 hours respectively.

The above results cannot necessarily be interpreted to mean that vitamins, and not the culture medium, are the all important factors in the germination of *Aspergillus*. Evidently, the spores of this fungus contain a very limited amount of stored food, which enables them to germinate in double distilled water. The vitamins, in this case, besides stimulating germination, certainly act as a food supply. The relative importance of these factors will be discussed later.

Microscopic examination of young germinating spores grown in nutrient solution with and without vitamins revealed certain marked morphological differences. The spores of the vitamin cultures were found to develop long, straight hyphae which

branched little. The branchlets are short, blunt, and uneven in diameter. In the controls the hyphae are comparatively short, but they show profuse branching. The difference between the different cultures does not become evident until at least nine hours after inoculation. FIGS. 3-7 illustrate this point.

Very marked differences were observed in a thirty-six hour culture (FIGS. 8-13). The control exhibited normal primary and secondary branching. Spores grown in the highest concentration of vitamins (40 mg./50 cc. of solution, circa 0.8 per cent) showed long straight hyphae, at the ends of which developed the usual primary and secondary branchlets, short and peculiarly blunt. Long, slender hyphae with exceedingly long cells grew out from these branches. Anastomosing between these secondary hyphae was frequently observed. The whole gave an impression as though growth, for some reason, had been temporarily arrested, and then suddenly resumed. Between the two extremes—control and most highly stimulated culture—all intermediate stages were found (FIGS. 6-11).

Anastomosing between different hyphae was occasionally observed in the stimulated cultures, but never in the controls. It was very abundant in the cases where the fungus was given vitamin powder as its only nitrogen source, and thus appears to be one of the characteristic effects of vitamins.

The determination of the economic coefficient of sugar showed that, in this regard, vitamin cultures behave in the same way as cultures which are stimulated by small doses of toxic salts: stimulation results in the raising of the economic coefficient of sugar, though in small amount.

TABLE 10. MG. MYCELIUM FORMED PER 100 MG. OF SUGAR USED

	<i>Control</i>	<i>5 mg.</i>	<i>10 mg.</i>	<i>25 mg.</i>	<i>40 mg.</i>
	35.4 mg.	35.88 mg.	35.83 mg.	36.2 mg.	38.1 mg.
	37.1	41.7	49.5	42.6	45.2
	36.3	34.1	37.0	41.4	39.3
	35.2	38.7	38.0	41.5	42.6
	<hr/>	<hr/>	<hr/>	<hr/>	<hr/>
Average	36.0 mg.	37.5 mg.	40.0 mg.	40.4 mg.	41.3 mg.

Richards (23) explains the raising of the economic coefficient of sugar as follows: "... the direct action of irritant substances ... which produce an increased growth of certain fungi is to

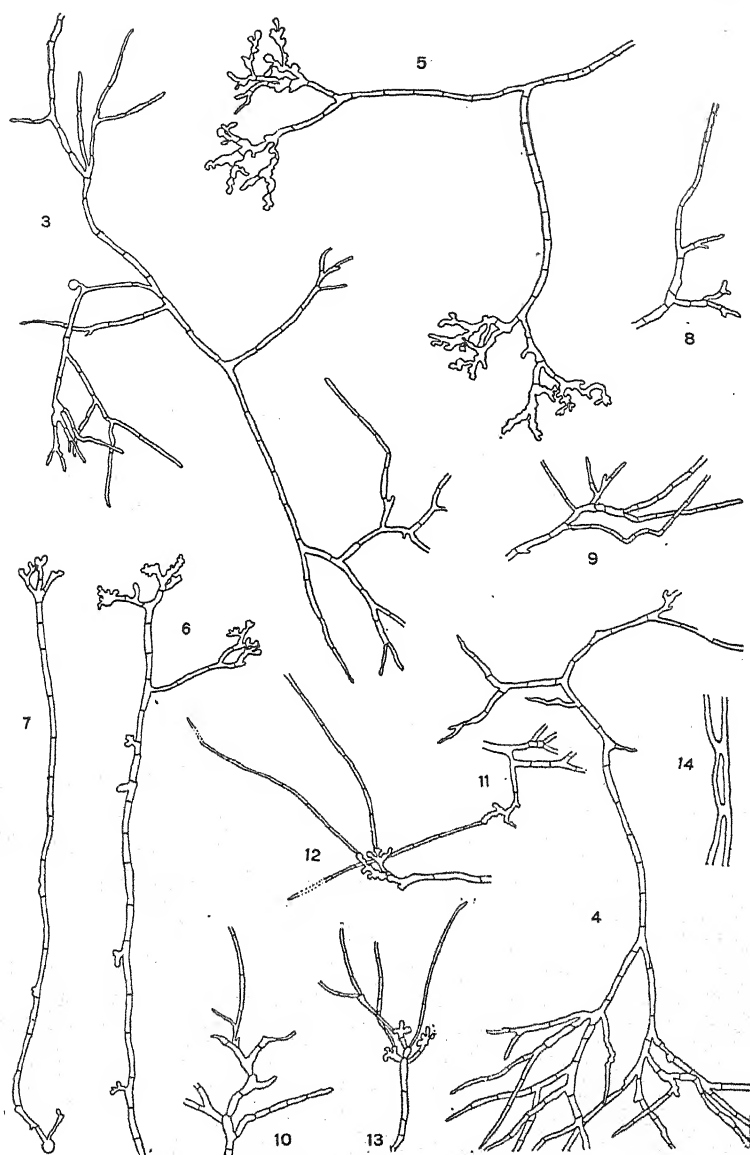
enable the latter to dispose more economically of the sugar used (i.e. to raise the economic coefficient of sugar) thereby permitting a more rapid production of dry substance in a given time." In the case of the vitamine cultures another explanation might possibly be resorted to: Funk (13) suggested that vitamines play an important rôle in the assimilation of carbohydrates. From his point of view it might be argued that in the vitamine cultures the fungus is able to assimilate the sugar more easily, and to use it more economically.

Richards (24), discussing the conidia formation in relation to the economic coefficient of sugar states that "Whether it is the more economical working of the protoplasm which inhibits the formation of conidia, or whether the absence of the latter results in less waste of energy in metabolism is perhaps a question, though probably most would agree that the spore-forming process is one that demands a greater expenditure of energy than the mere vegetative growth of the hyphae." This explanation holds good in all cases where stimulation expresses itself in increased vegetative growth, and inhibition of the reproductive factor. For vitamine cultures, where both phases of growth are stimulated, the explanation of the phenomenon has evidently to be sought elsewhere.

The acidity of the stimulated cultures was found to be less than that of the controls. It was determined by titration with standardized N/20 sodium hydroxide. No determinations of the hydrogen-ion concentrations were made. The filtrate left at the end of the experiment was made up to 100 cc., and an aliquot portion titrated, phenolphthalein being used as indicator. Upon deducting the original acidity of the medium from the final acidity, the acid formed in the metabolism was determined. The value of this amount has to be considered as relative only, inasmuch as some acid may be broken down further, or taken up again in the anabolism of the fungus.

TABLE II. CC. N/20 ACID FORMED PER 100 MG. OF MYCELIUM (DRY WEIGHT)

	<i>Control</i>	<i>2.5 mg.</i>	<i>5 mg.</i>	<i>10 mg.</i>	<i>25 mg.</i>	<i>40 mg.</i>
	3.24	2.33	2.95	1.70	1.60	1.02
	1.64	1.81	1.41	1.13	1.38	1.35
	2.34	2.40	2.15	2.37	1.97	1.54
Average	2.40	2.18	2.17	1.73	1.65	1.30



FIGS. 3-14. 3. Control, nine hours after sowing. 4-7. Same, but with 2.5-, 5-, 10-, 25-, and 40-mg. vitamine preparation per 50 cc. culture solution respectively. 8. Control, growing tips of hyphae thirty-six hours after sowing. 9-13. Same, but with 2.5-, 5-, 10-, 25-, and 40-mg. vitamine per cc. culture solution respectively. 14. Anastomosing hyphae as seen in cultures of high vitamine content.

## THE EFFECTS OF VITAMINE POWDER ON WHEAT

Clean, synthetic sand was placed in small glass jars, and sterilized in the hot air oven at 150° C. for one hour. Germinating grains of *Triticum vulgare* (white winter wheat) were planted in the jars. Distilled water, instead of nutrient solution was used in these experiments, so as to make the grains entirely dependent upon the endosperm, and the vitamine powder. Drying up was prevented by keeping moist filter papers over the jars during the first few days, and by placing bell-jars over the cultures. After ten days the wheat seedlings were removed from the jars, the sand carefully washed out from the roots, and the epicotyl measured. The remainder of the endosperm was removed, and the seedling dried to constant weight in a hot air oven at 70° C. The results are summarized in TABLE 12.

TABLE 12. EFFECTS OF VITAMINE POWDER ON WHEAT

	Control	20 mg. Vit./50 cc.	40 mg. Vit./50 cc
Seedlings counted	172	228	137
Average length, cm.	11.1	13.06	13.8
Average weight, mg.	19.8	22.0	20.3
Av. weight per cm., mg.	1.78	1.67	1.36

As had previously been observed by Bottomley (2), the vitamine powder (or auximone) stimulates the growth of wheat seedlings. It is a well known fact that germinating wheat contains vitamins. Just how and where these growth accessory substances are produced is an open question. From the above experiments it appears that the wheat can assimilate more vitamins than it has at its disposition during germination. Apparently vitamine powder does not produce any inhibition of growth, even if the concentration is fairly high. A limiting factor of growth may be the luxuriant development of bacteria in high concentrations of vitamins. This troublesome factor was never met with in the *Aspergillus* cultures, probably on account of the high acidity of the medium. Bottomley would possibly attribute the stimulation of wheat, observed in the above experiments, not to the vitamins directly, but to the bacteria from which growth accessory substances are supposed to diffuse out into the medium.

The macroscopic appearance of the epicotyls of seedlings grown in distilled water with or without vitamins showed very

little difference. All the plants appeared dark green and healthy. The seedlings of the stimulated cultures often showed a poorly developed root system. They differed furthermore from the controls by being very weak: a slight draught proved sufficient to bend the plantlets. Time did not permit the study of the anatomy of seedlings grown in different solutions.

The calculation of the average weight per centimeter is of relative value, inasmuch as only the length, but not the width of the leaf could be taken into account. The numbers are of interest in connection with the suggestion that the seedlings of the vitamine cultures have poor supporting tissue.

Bottomley observed that if the endosperm of wheat is removed at an early stage the seedlings do not develop normally. To verify this point the endosperm of wheat seedlings grown on Knop's solution with and without vitamins was removed when the epicotyl was about one inch long. The plantlets of all the different cultures seemed to develop normally, although more slowly than if the endosperm was present. The normal development of seedlings grown in mineral solutions explains itself probably by the fact that the embryo of wheat is very rich in vitamins, and that it can draw upon this supply for a considerable time.

#### THE EFFECTS OF VITAMINE POWDER ON *LEMNA* MINOR

The cultures were grown in black painted, sterilized battery jars. Knop's solution was used as medium. The experiment was set up as follows:

- |      |                     |                                         |
|------|---------------------|-----------------------------------------|
| I.   | Control:            | 600 cc. of solution.                    |
| II.  | 600 cc. of solution | + 240 mg. of Vit. powder, unsterilized. |
| III. | 600 " " "           | + 240 " " " " sterilized.               |
| IV.  | 600 " " "           | + 480 " " " " unsterilized.             |
| V.   | 600 " " "           | + 480 " " " " sterilized.               |

Twenty-five mature *Lemna* plants, each consisting of three leaflets, were placed in each jar. The culture was grown for three weeks. Once a week the leaflets were counted, the solutions changed, and the jars thoroughly cleaned. This proved to be necessary, inasmuch as a thick bacterial scum developed regularly in all the solutions containing any vitamine. Sterilization of the media helped little: the bacteria were apparently introduced with the *Lemna* plants, and the acidity of the culture

solution was not sufficiently high to check the development of these organisms.

After the first week the control plants had practically all broken up into single leaflets which looked yellowish and sickly. The plants grown in solutions II, III, IV and V, on the other hand, were dark green. Each one consisted of three to five leaflets. As TABLE 13 shows, the number of control plants increased hardly at all during the two following weeks, while the reproduction of the plants of the remaining cultures appeared markedly stimulated.

TABLE 13. STIMULATION OF LEMNA MINOR

	Control	II	III	IV	V
One week	96	119	128	146	141
Two weeks	110	162	164	169	199
Three weeks after inoculation	126	189	197	243	297

Contrary to expectation, the vitamine culture during the first week of growth showed marked stimulation of vegetative reproduction, while the second week brought a slowing down of this process. The maximum reproduction in the case of IV and V was obtained during the third week.

These observations only partly confirm the results of Bottomley, who found his maximum reaction to occur during the second and third weeks. Bottomley's tables furthermore show a much more marked stimulation than was obtained in the above experiments. The luxuriant development of bacteria in the vitamine cultures constitutes possibly a limiting factor on the rate of growth. On the other hand, it might be argued that since Bottomley obtained his growth promoting substances from bacterial cultures, the stimulation in the above experiments might be due, not to the vitamins as such, but rather to substances which diffuse into the medium from bacterial cells. Reasoning from analogy with the *Aspergillus* and wheat cultures, this suggestion will hardly hold good.

## DISCUSSION

*Aspergillus niger* develops normally in Pfeffer's solution without any accessory substances. Both vegetative growth and reproduction are accelerated by the addition of small amounts of vitamine B to the medium. The main stimulating effects of

the growth accessory substances upon *Aspergillus niger* were found to occur during the first five hours after inoculation. The ratio of the dry weights of the mycelial felts of the stimulated cultures, and the controls is practically constant, whether the cultures be reaped forty hours, three and one-half days, or twelve days after inoculation. In this regard, the results of the experiments described in this paper are at variance with the observations of Lepeschkin and Linossier, who found that vitamins have a stimulating effect upon *Penicillium glaucum* and *Oidium lactis* only during the very earliest stages of growth.

In the opinion of Steinberg (27) the cause of stimulation is the increased acidity of the medium, due to the addition of certain substances. The results of the experiments described in this paper might be interpreted along this line (TABLE I), but there are reasons to believe that the matter is more complicated.

The effect of vitamin B upon *Aspergillus niger* may be catalytic. If Funk's conception that vitamins are of utmost importance in the carbohydrate metabolism is correct, the sugar in the stimulated cultures would be more available to the organism. The economic coefficient of sugar would thus be raised: the different phases of growth could be carried on with greater ease and rapidity. To prove the point whether vitamin B acts as a catalyst in the sense that it renders the carbohydrate more available to the organism, it would be necessary to determine the amount of vitamin still present at the end of an experiment. For obvious reasons, such a determination is involved with great difficulties, if not impracticable.

It is most probable that the effects of vitamin B are those of an increased organic food supply, or that the substance acts as a stimulant in the sense that small amounts of toxic substances act as stimulants.

Several considerations are in favor of the former conception. Stimulation of the vegetative growth, expressed by the increased dry weights of the mycelial felts is much more nearly quantitative than is the case for instance with a typical zinc culture (TABLES I, 3, 4, FIG. 1). Furthermore, *Aspergillus niger* grows profusely in media containing vitamin powder as the only nitrogen source (TABLE 2). There is no definite optimum nor maximum concentration of the vitamin in the culture solution. Fleming (11) suggested that the addition of organic nitrogen to



a medium containing only inorganic nitrogen might cause stimulation. To determine the correctness of this conception it will be necessary to make quantitative analyses of the nitrogen content, as described by Latham (17). On the other hand stimulation is found with very small doses of the vitamine preparation, where the added nitrogen content can hardly play a significant rôle.

However, taking into consideration the raising of the economic coefficient of sugar, and the lowering of the total acidity, it seems more logical to suppose that the effects of vitamine B are similar to those obtained by the addition of minute doses of toxic substances to the culture medium. The main difference between vitamine and zinc cultures lies in the fact that, in the case of the former, sporulation is never suppressed, nor even inhibited, but on the contrary stimulated, while, at the same time, the development of the mycelium is not as markedly stimulated. These two observations do not constitute a point of vital difference between the vitamine and the zinc cultures. They may easily be explained by supposing that two factors are brought into play by the addition of vitamine powder to the medium, one factor stimulating vegetative growth, the other one important in reproduction. It is easily conceivable that the vegetative factor is limited by the reproductive factor. It appears that the vegetative factor is at its optimum if the concentration of the vitamins is lowest, i.e. at 0.05 per cent. TABLE I and FIG. 1 show that comparatively higher weights of the mycelia are obtained with this concentration than with the next higher. A further argument in favor of the double stimulation effect is the fact that the germination of spores is markedly stimulated by very low concentrations of vitamins (TABLES 5, 6). During these earliest stages of growth the vegetative factor alone is at work.

These arguments lead the writer to believe that the effects of water soluble vitamine B upon the vegetative growth of *Aspergillus niger* are similar to those produced by small doses of toxic substances.

This work was done under the guidance of Professor Herbert M. Richards, for whose kind advice and criticism the writer is greatly indebted.

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May 1924

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# The embryogeny of *Cephalotaxus Fortunei*\*

JOHN T. BUCHHOLZ

(WITH PLATE IO AND TWO TEXT FIGURES)

The embryogeny of *Cephalotaxus* is of very great interest in a study of the comparative morphology of conifers. *Cephalotaxus* is usually included among the Taxineae, but the embryo has been reported as having certain points of comparison to the Abietineous type of embryo: it has a terminal cap which may be homologous with the embryo cap of Araucarians and it furnishes a key to the homologies between the embryos of the other Taxineae and Podocarpaceae. The conclusions reached in this paper apply to embryogeny only, and it is fully realized that they must be considered in connection with other morphological facts in any final decision concerning the proper affinities of this genus. As such we believe that comparisons based on the embryogeny should be among the most important considerations, and this study aims to emphasize this phase in the morphology. The interpretation given here, while a new one, was suggested in its main outline in the writer's resumé of conifer embryogeny (1920) and finds much additional support from the first-hand examination of this material.

## MATERIAL AND METHODS

The material for this investigation was kindly furnished by Dr. W. C. Coker in 1921, from trees growing in the Arboretum at Chapel Hill, North Carolina. Living twigs of *Cephalotaxus Fortunei* were sent to the writer in four collections, from June 19 to August 3, 1921. The gametophytes were removed and their embryos dissected out in the living condition with the aid of a Greenough binocular microscope under a sugar solution of about  $\frac{1}{2}$  gram molecular concentration. These were placed immediately in a killing and preserving fluid consisting of 6 per cent formalin in 50 per cent alcohol. In this condition they were preserved for several years. In the technique of mounting,

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the embryos were washed and then stained for fifteen minutes in Delafield's haemotoxylin, de-stained slightly with acidulated water, after which they were again washed, placed in 10 per cent glycerine and left for several days in the open, protected from dust, until the glycerine became fully concentrated. The glycerine was washed out with several changes of 95 per cent alcohol, from which they were transferred to absolute alcohol. From this they were mounted in diaphane (a new mounting medium manufactured by the Will Corporation, Rochester). A previous test of this mounting medium with algae indicated that it would be best to transfer the material into diaphane gradually, first placing it in a mixture of half diaphane, half absolute alcohol. The embryos were therefore placed on a slide from the absolute alcohol and this 50:50 solution dropped on them immediately. The alcohol evaporates rapidly, and may be followed in from one to three minutes by the pure diaphane medium, and covered.

This medium seems to possess most of the advantages of Venetian turpentine used in the writer's previous work, and saves a little time. It also hardens faster than Venetian turpentine, and does not emulsify when moisture is absorbed from the air. The blue stain of the haemotoxylin is rendered brown, which is of no disadvantage for direct observation and has some distinct advantages in photographic work. Sections were made of the embryos in the last collection. These were killed in formalin-alcohol, cut in paraffin, stained with Haidenhain's haemotoxylin, counterstained with gold orange and mounted in Canada balsam.

The photomicrographs were made with an Edinger apparatus, using Bausch and Lomb Micro-tessars stopped down, and the low power microscope combination of the apparatus ( $\frac{2}{3}$  inch objective and 8 $\times$  aplanoscopic ocular) with Cramer's contrast plates.

#### PREVIOUS INVESTIGATIONS

*Cephalotaxus* has been investigated morphologically by Strasburger (1879), Arnoldi (1900), Coker (1907), and Lawson (1907). The various other investigations of this species did not include accounts of the embryogeny. Strasburger's observations begin with the organized proembryo, while Arnoldi, Coker and Lawson included earlier stages. The first three of these in-

investigators included only *Cephalotaxus Fortunei*, while Lawson was largely concerned with *Cephalotaxus drupacea*, though he also examined material of the former. There seem to be no important differences between these two species. The proembryo stages are briefly outlined below in order to make the present description more complete, but the writer's observations were confined to the stages after the walls were formed and the suspensor cells were beginning to elongate.

#### PROEMBRYO

The proembryo of *Cephalotaxus* has been described by the above mentioned investigators and in the main outline these accounts are in substantial agreement. A good summarized account of this is given by Coulter and Chamberlain (1910). All of the cells formed are confined to the lower portions of the archegonia, which are very long and narrow, and decidedly pointed at the lower end. Walls do not appear until after sixteen free nuclei have been formed. The first walls appear on the division spindles after the four simultaneous nuclear divisions. Additional cells are soon formed so that at least thirty-two cells or probably more, are formed in the entire zygote before the suspensor elongates. As soon as the suspensor cells are distinguishable by their slight enlargement, we may recognize the embryo as organized into four groups of cells, some of them arranged more or less in tiers. This tier arrangement is not at all even as in Abietineae, and the further meristematic activity of the different regions which might be assigned to various tiers of cells make these stages much more irregular and variable in appearance than in such forms as *Pinus*.

The thirty-two cells are shown by Coker (1907) in his figure 19, and these are crowded into the base of this narrow cone-shaped archegonium with a single cell at the point, overlaid by the other cells, so that passing upward, one observes more and more cells somewhat unevenly placed, but all crowded into the lower third or two-fifths of the archegonium.

The large cell at the bottom of the archegonium forms a penetrating cap which appears to protect the primary embryo, much as a root cap protects an advancing root tip. The several adjacent cells above this, below the mass of embryonic meristem also remain large and inactive and are to be included with this lower one, as a group of cells forming the cap.

The next group of cells above the deciduous cap is a very active mass of cells which become small on account of their meristematic activity and are somewhat irregular in their arrangement. These cells which ultimately contribute the primary embryo can therefore not be spoken of strictly as a tier of cells. Above these is a third more even tier of from five to seven or more cells which form the primary suspensor and can be recognized as soon as these cells begin to elongate, while a fourth group of cells above the suspensor tier is composed of cells which are soon actively dividing, constituting the "rosette" cells. From all of the four accounts of the proembryo we have no evidence of the existence of a tier of free nuclei above this rosette group, another point wherein the proembryo of *Cephalotaxus* differs from that of Abietineae. In a sense the rosette cells of *Cephalotaxus* are therefore not strictly homologous to the rosette cells of the pine embryo, but since these are the uppermost walled cells in both cases above which the basal plate appears, we will speak of them as the rosette cells in this discussion.

#### DESCRIPTION OF OBSERVED STAGES

The present investigation begins with young embryos of the type shown in FIG. 1. Here we see two neighboring embryo systems coming from adjacent archegonia. A few stages younger than these (before suspensor elongation) were found, but could not be reproduced satisfactorily by photography and were therefore omitted.

In FIG. 1, the cap cells may be seen on each of the primary embryos. Above these are the groups of meristematic cells which give rise to the embryos proper, and above these are the primary suspensors which are made up of five to eight collateral elongating cells. A group of rosette cells is shown above this, and the plug of opaque substance which forms in the egg above the embryo is present in the zygote shown at the left. This probably corresponds to the basal plate of Abietineae. In the embryo to the right, this was lost in dissection.

The cavity of the gametophyte, into which the primary embryos are pushed by their suspensors, is formed by the corrosive action of enzymes which are secreted from some or all parts of the embryo. While mechanical action of the suspensors keeps the several embryos pushed forward as far as possible

in this cavity, the digestion actually precedes this mechanical action. Lawson (1907) describes a clear space in advance of the embryo tip, and in a study of the pine and other conifers, it has appeared certain to the writer that the suspensor does not force the embryo in a crushing manner through the firm living gametophyte tissue. Since these studies were made from dissections, no such sectional views as those mentioned by Lawson were observed. From the ease with which the embryos were removed there was very little or no evidence which would indicate that the suspensors were mechanically pushing their embryos forward faster than the digestive action of the enzymes opened up the cavity occupied by the embryos. Doubtless they crush aside the remains of collapsed cells after the enzymatic action has rendered the gametophyte tissue spongy.

The primary suspensors are at first straight and rather stiff, but in time they become coiled and twisted. They continue to elongate without the addition of a secondary suspensor in the form of embryonal tubes, until they have reached a great length, those in FIG. 4 measuring over 7 mm. long, counting the twists. Thus the embryonic cell group is pushed forward far into the gametophyte tissue, and during the stages represented between FIGS. 1 and 5, the large cap cell is usually lost. According to Lawson, it is lost very early in the succeeding stages. FIG. 4 represents the embryo systems from two adjacent archegonia, which had a very even start and developed side by side. It may be seen in FIG. 5, that the larger of the two primary embryos has lost its largest cap cell while the smaller still retains all of the cap. This is probably a late stage in which to find this organ present. In FIG. 3, an embryo is shown probably without its largest cap cell (though this may have been loosely attached and lost in the dissection). It is interesting to note that in the writer's earlier stages (FIGS. 1 and 3) the nuclei of these suspensor cells, together with a dense mass of cytoplasm, are situated in the lower end of the suspensor, i. e., near the mass of embryonic cells, but by the time the stage of FIG. 5 is reached they are usually not found. This position of the nucleus was also observed by the writer in practically all conifer embryos which he has had occasion to examine.

It is especially interesting to note that several embryos from different eggs are engaged in an embryonic "struggle for exist-



ence" and the suspensor is the weapon by which the adversaries are overcome. As the embryos grow longer (FIGS. 7-8), they give off a massive suspensor of embryonal tubes as in other conifers. These originate from the cells of the primary embryo nearest the older portions of the suspensor. These successive waves of elongating cells sometimes become entangled with their adversaries and sooner or later the vanquished are pushed back to the archegonial region until only one, the successful embryo, occupies the favorable position, which insures its survival as the embryo of the seed. Embryonic Selection is a special form of Developmental Selection and its significance in evolution has been outlined elsewhere (Buchholz, 1922).

#### THE EMBRYOS DERIVED FROM THE ROSETTE REGION

An outstanding new item in the present investigation is the demonstration that usually other embryos are derived from the rosette region. The group of rosette cells (upper part of FIGS. 1, 2, and 4) are all meristematic, and when followed through later stages (FIGS. 7-9) become active, developing into embryos. They are devoid of a primary suspensor, but soon become multicelled and of good size, sending out the embryonal tubes of a secondary suspensor (FIGS. 7-9), thus demonstrating that they are in the nature of real embryos. Their orientation is variable and probably they grow out in any direction. They do not possess the deciduous cap cells found in the primary embryo.

It is clear that in *Cephalotaxus* each zygote gives rise to several rosette embryos in addition to the primary embryo, which demonstrates that we are dealing with a compound embryo, that we have here a partially suppressed form of cleavage polyembryony.

FIG. 8 shows an embryo which is double. There is one large embryo and beside it a small one, as if to indicate an instance of cleavage polyembryony in the primary embryo. It is more probable that these are the embryos of two archegonia, as if FIG. 5 had developed to a later stage. Of course, it is not impossible that the main embryo may divide, but aside from FIG. 9, no apparent evidences of cleavage in the primary embryo have come to the writer's notice in the course of these studies, and it seems certain that cleavage of the primary zygote is at least not frequent. From the external appearances of the embryos

there is no evidence for the existence of an apical cell at any stage in the primary embryo, and there is also no external evidence of an apical cell in the rosette embryos.

Sections of later stages in the primary embryo are shown in FIGS. 10 to 12. The evidence which we have here indicates that the stem tip meristem is the last region of the embryo to become organized. In the Pine, the stem tip appears as a slight swelling before there is any evidence of the cotyledons, and while it does not develop further, it remains as a dome-shaped protuberance from this stage on. FIG. 10 shows the plerome, periblem, and dermatogen all organized. The latter extends well down the sides of the root cap. In the pine, the plerome of the root tip is the first region to differentiate and the dermatogen is not definite until much later. The cotyledon primordia are organized, and the plerome strands are beginning to extend into the cotyledons. The periblem is indicated between the dermatogen and plerome but is not sharply differentiated at the point where it joins the root cap, and the root cap further merges insensibly with the suspensor.

In the next stage observed (FIG. 11), the periblem is becoming more distinctly differentiated from the suspensor, but its separation is not sharp even in FIG. 12. The epidermis in FIG. 12 may be seen to extend well down the sides of the root cap to the suspensor region and it appears that the periblem and root cap are a continuous tissue of cells which merely become larger and more vacuolated as one passes from the plerome to the suspensor region. This entire region of the embryo is short compared with that of the pine embryo, where the periblem of the root tip and the root cap constitute nearly half of the length of the embryo at the time when the seed is ready to be shed.

The triangular mass of substance above the flat stem tip between the cotyledons (FIGS. 11, 12) is composed of a mass of undigested cell walls which have accumulated from the disintegrated cells of the surrounding gametophyte tissue. In the embryo of FIG. 10, a similar plug of some kind was removed with difficulty during the dissection. This object was found in all the embryos which were sectioned, but it is in no way derived from embryonic tissue.

The largest embryos which were sectioned showed a hollow pith cavity in the middle of the plerome region as indicated in

FIG. 12. This was found in all other embryos of this size. It is evidently formed by a breaking down of the cells of the plerome, and is accompanied by a swelling of the central region of the embryo. The embryo chosen for illustration in FIG. 12 did not show the swelling as much as some others. About twenty of these later embryos which were removed from the ovules all proved to possess two cotyledons.

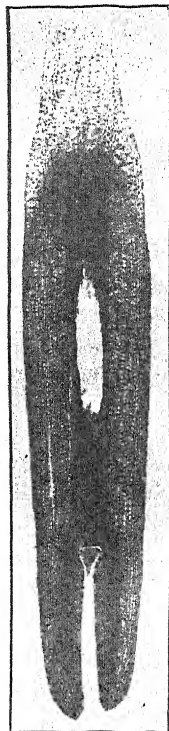
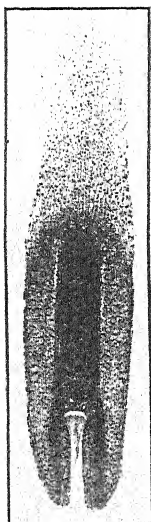


FIG. 11. Section of older embryo of *Cephalotaxus* showing cotyledons half grown, periblen sharply differentiated from plerome and less distinctly from root cap. The stem tip is still flat. A plug of crushed cells derived from the disintegrated gametophyte tissues, lodged above the embryo body between the cotyledons, is not a part of the embryo.  $\times 18$ .

FIG. 12. Embryo of seed in a stage nearly fully developed, but in which the stem tip is still flat and undifferentiated. Periblen has become more sharply differentiated from plerome, and the dermatogen extends distinctly over root cap to the region of the suspensor. A pith cavity of broken down cells has appeared in the center of the plerome.  $\times 18$ .

## DISCUSSION

Previous investigators have compared the proembryo to that of the pine. There are, however, many points of difference and the homology between the embryogeny of *Cephalotaxus* and that of *Pinus* is not so evident from appearances. The first walls of the pine proembryo come in after eight free nuclei are formed, while in *Cephalotaxus* there are sixteen free nuclei before the cell walls appear. The terminal four cells in the pine proembryo function actively as apical cells for the respective four embryos while in *Cephalotaxus* the lowest cell which corresponds to the apical cell of the primary embryo in position is a single cell. It enlarges and becomes the terminal cell of the group constituting the cap. Finally we have a proembryo of many cells rather than one of sixteen cells at the time when the suspensors begin to elongate, and there appears to be no apical cell stage at all in the *Cephalotaxus* embryo.

The writer feels convinced from this study that the key to the real homologies between the parts of the embryo of *Cephalotaxus* and those of pines and other conifers lies in its cleavage polyembryony.

If embryo initials are represented by the proembryo at the time when the first walls are formed, then *Cephalotaxus*, which has walls organized around all of its nuclei when walls first appear, represents sixteen potential embryo initials. If any of the subsequent divisions represent still further organization of greater cleavage polyembryony there may be even more, as is probably the case in *Sciadopitys* (Buchholz, 1920). Of course, *Cephalotaxus* has practically eliminated the cleavage polyembryony for the primary embryo; at least the writer found only one instance (FIG. 8) where two or more embryos could have been formed by division of the meristematic mass of cells next to the cap cell, and this one is extremely doubtful. The writer believes that the organization of this cap was partially, if not largely instrumental in the elimination of cleavage polyembryony during the early stages. Lawson (1907) states that "the early meristematic activity of the (primary) embryo may explain the necessity for the development of the terminal cells into a penetrating cap. This explanation finds support in the fact that the cap cells are thrown off very soon after the suspensors are developed." At any rate, if excessive cleavage polyembryony existed

in forms ancestral to *Cephalotaxus*, the cap was probably not then present, and its origin may have been associated with the suppression of both cleavage polyembryony and the apical-cell stage. The present protective function as an organ of penetration or even as a secreting organ is not denied in assigning this rôle to the cap cells, but the writer is also convinced that this is not a very essential organ, for embryos frequently shed their caps in early stages and most conifers have no such organ at any stage of their embryogeny.

The cap cells are therefore not homologous with anything in the embryo of the pine unless they represent one or more abortive embryo initials. The mass of cells of the embryo proper above the cap cells represents a large number of the embryo units (embryo initials) corresponding to the four which separate in *Pinus* and the probably larger number found in other conifers such as *Sciadopitys* (Buchholz, 1920). The suspensor cells may represent the first cells cut off by some of the embryo initials of this group, or more probably they represent still other embryo initials which elongate. In the pine, the rosette cells which are unquestionably embryo initials sometimes elongate as suspensor cells in such a manner. That the rosette cells are embryo initials is fully demonstrated.

Though the group of rosette cells above the suspensors were observed by others, they have apparently not been studied, at least their destiny as embryo forming cells was not suspected. Strasburger (1879), Coker (1907), and Lawson (1907) mention them as a group of rosette cells, but followed them no further. Coker agrees with Strasburger's observation in noting these rosette cells, probably of the stage shown in FIG. 2.

While Strasburger figured the early stages of these rosette embryos without comment, Coker and Lawson both figured small secondary embryos above the primary one in an older stage, but regarded them as the result of later fertilization of archegonia, which is also possible in the sections which they figured. Lawson considered them as possible cases of embryos budding from "the main group of embryo cells and the formation of small secondary embryos. These however, are not frequently found. As a rule there is but one embryo formed from a single archegonium." It is likely that both Lawson and Coker were dealing with some of these secondary or rosette embryos.

The existence of these active rosette embryos associates *Cephalotaxus* with the group of conifers which have a modified form of cleavage polyembryony. It is from the behavior of these rosette cells that we obtain a definite clew to the polyembryonic history of *Cephalotaxus*. Being uppermost in their position these are probably homologous with the rosette embryos of the pine if we disregard the free nuclei above the rosette cells in *Abietineae*. When cleavage polyembryony was suppressed in the lower portion of the embryo system, this did not do away with cleavage polyembryony in the rosette group. At least we are better able to make comparisons between the embryo of *Cephalotaxus* and those of *Abietineae*, and other conifers, when we consider the nature of these secondary rosette embryos in the light of a polyembryonic origin.

This also adds to our evidence for the view that cleavage polyembryony is a condition through which the Coniferales have passed in their evolution, for certainly *Cephalotaxus* supplies us with satisfactory ontogenetic evidence of this kind. A further discussion of this very fascinating problem of the origin and evolution of cleavage polyembryony will be treated by the writer in another paper.\* It may be stated here that the origin of this condition represents an episode in the evolution of conifers, having to do with the beginnings of siphonogamy in the origin of seeds.

#### SUMMARY

We have, in *Cephalotaxus*, an embryo which is derived from a condition of cleavage polyembryony. Most, if not all, of the early cells of the proembryo are to be regarded as embryo initials. Of these, the terminal cells do not form embryos but go to form the cap instead. The next group of proembryonic cells above the cap combine to form a single embryo. The primary suspensor is formed from a tier of cells above these, and becomes very long, while the uppermost tier, the rosette cells, are the only ones which retain fully their separate embryo-forming capacity, usually giving rise to several rosette embryos. No certain evidence of cleavage of the primary embryo was observed.

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\* Concerning the origin of cleavage polyembryony in conifers. To appear in Botanical Gazette.

In the later embryo the stem tip is differentiated late, long after the dermatogen, periblem, plerome, root cap, and cotyledons have become fully organized,—in a stage later than any in the figures shown in this treatise. The dermatogen appears early and extends down over the root cap to the region of the suspensor. A cavity is formed in the later stages by a breaking down of cells in the middle of the plerome region. The embryos usually have two cotyledons.

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CEPHALOTAXUS FORTUNEI

## Description of plate 10

FIG. 1. Two embryos from neighboring archegonia dissected out of gametophyte and mounted. Beginning below, they show the cap cells, next a group of cells forming primary embryo, above these the elongating suspensor cells, and above the suspensors a group of cells forming the rosette embryo. In the embryo to the left is a mass of deeply staining substance found above the rosette in the archegonium (which was removed by the dissection in the embryo to the right). This probably corresponds to the basal plate of *Abietineae*.  $\times 56$ .

FIG. 2. Dissection of slightly younger stage than FIG. 1, showing rosette embryos slightly separated by dissection. Suspensor cells have their lower ends slightly enlarged and nearly all of the nuclei are found here. The primary embryo with its cap cells was lost in the dissection.  $\times 56$ .

FIG. 3. Embryo of the same age as FIG. 2 with primary embryo in position but with the terminal member of the group of cap cells missing, probably lost in dissection.  $\times 56$ .

FIG. 4. Embryos of two adjoining archegonia with suspensors fully elongated. The rosette embryos are developing from the rosette above and are shown enlarged in FIG. 6. Embryonal tubes have not begun to elongate to form the secondary portion of the suspensor.  $\times 18$ .

FIG. 5. More detailed view of primary embryos of FIG. 4. The embryo to the left still possesses the terminal cap cell, while the larger one to the right has discarded its largest cap cell.  $\times 56$ .

FIG. 6. More detailed view of rosette embryos of FIG. 4, showing the embryonal tubes forming a secondary suspensor. No primary suspensor is developed for the rosette embryos.  $\times 56$ .

FIG. 7. Older embryo with massive secondary suspensor well developed and with older group of five rosette embryos above, in various stages.  $\times 10$ .

FIG. 8. Embryos younger than FIG. 7, with apparently two primary embryos formed side by side (?) and a single very irregular rosette embryo above. The rosette embryos shown in FIG. 9 belong with these.  $\times 29$ .

FIG. 9. Part of the rosette embryo group dissected away from the embryo system of FIG. 8. Note absence of cap and primary suspensor, the lobed and irregular character of the rosette embryos which have developed very unequally.  $\times 56$ .

FIG. 10. Section of embryo of *Cephalotaxus* with body regions organized and cotyledons developing. Stem tip is unorganized, plerome is distinguishable from periblem, but periblem, root cap and suspensor merge into each other. Dermatogen appears to extend down over root cap.  $\times 18$ .



## Studies on the flora of northern South America—VI\*

H. A. GLEASON

### NEW OR NOTEWORTHY SPECIES OF MELASTOMATACEAE

Generic characters seem to be sharply marked in the majority of melastomataceous genera. The chief exceptions are found in the tribe Miconieae, where genera are distinguished largely on the position of the inflorescence and the shape of the petals. Here also are found many cases of remarkable similarity in habit between species of different genera, such as *Leandra* and *Miconia*, and it becomes extremely difficult or even impossible to place some immature or fruiting specimens into a genus with confidence. Within the genus *Miconia*, with well over six hundred species, the eleven sections are not always easily differentiated. They are characterized by the shape and dehiscence of the anthers, and there seems to be an almost continuous series of anther-shapes between the subulate, attenuate anthers of *Tamonea* and the linear ones of *Eumiconia*, and from the latter to the oblong, small-pored anthers of *Amblyarrhena*, and on to the obovate, large-pored anthers of *Cremanium*. Sections *Jucunda*, *Tamonea*, and *Adenodesma* are very close, as are also *Cremanium* and *Chaenopleura*. I have found no good evidence to warrant any segregation of the genus.

It is in most cases absolutely necessary to soften flowers by boiling and to make careful dissections in order to determine with any degree of accuracy the structure of the stamens. This has been done for all of the species described below, excepting a very few in which the stamens are not mentioned. All measurements of stamens, styles, seeds, and other small floral organs have been made with an eye-piece micrometer from boiled material, and have always been taken from the type specimen only.

Within a single flower, deviations in measurements from the stated dimensions are negligible, and rarely amount to as much as 5 per cent. Greater variations are found between different flowers of the same plant, or between different plants of the same

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\* Contributions from the New York Botanical Garden, no. 274.

species. These are probably due chiefly to age, but we do not know anything about the relative amount of elongation that takes place in the flower of a melastome during anthesis. It follows, therefore, that the measurements here given, although accurate in themselves, might not be repeated precisely in any other dissection.

There are similar variations in size in the leaves of any herbarium specimen. The measurements given here are taken, when expressed without any variation, from the largest leaf, or, when a range of size is indicated, from typical foliage leaves situated below the inflorescence. It is worthy of note that few sheets are examined in which the size of the leaves is as great as that given by Cogniaux, who seems to have allowed for an increase in size of those leaves farther down the stem and consequently not collected in a specimen of ordinary size.

*Pterogastra glabra* n. sp. Herbaceous, apparently erect, sparingly branched above; stems green, slender, narrowly 4-alate, glabrous, or very rarely with a few minute appressed hairs on the wings, sparsely setose at the nodes; petioles glabrous, 2-3 mm. long; leaf-blades firm, oblong-lanceolate, 30-45 mm. long, 5-9 mm. wide, acute, often minutely aristate, minutely crenulate and setose-ciliate with erect hairs nearly 1 mm. long, acute at base, bright green and glabrous on both sides, 3-nerved, the veinlets very obscure; flowers 5-merous, few, in loose, open, bracteate cymes terminating the stem and branches; peduncles narrowly 4-alate or merely quadrangular; bracts subulate, 2 mm. long, ciliate; pedicels 2 mm. long, glabrous; hypanthium bright green, campanulate, 6-7 mm. long, prominently 10-nerved, glabrous, or the 5 nerves opposite the sepals somewhat stronger and rarely appressed-spinulose; sepals green, herbaceous, triangular-lanceolate, 6 mm. long, 2 mm. wide at base, acute, aristate with a seta 1 mm. long, prominently setose-ciliate, obscurely reticulate; petals apparently blue, broadly obovate, about 13 mm. long, finely ciliate; anthers linear-subulate, yellow, 10 or 6 mm. long, arcuate retrorsely, opening by a minute terminal pore; connective slender, prolonged 2 or 0.5 mm.; bearing 2 stout, blunt, rounded, anterior appendages 0.5-0.7 mm. long; filaments slender, 6 or 5 mm. long; ovary ellipsoid, 4 mm. long, with a terminal circle of slender, glandless setae 0.7 mm. long; style terete, 3.5 mm. long. FIG. 1.

Type, *Pittier 10,577*, collected in wet savannas, Mene Grande, State of Zulia, Venezuela, 28 Oct. 1922, and deposited in the herbarium of the New York Botanical Garden. It is

closely related to *P. divaricata* (Bonpl.) Naud., but differs in its glabrous leaf-surface, essentially glabrous stem, almost wingless, usually glabrous hypanthium, and shorter ovarial setae.



FIG. 1. *Pterogastra glabra* Gleason, flower, bud, and leaves,  $\times 2$ .

*TIBOUCHINA GRACILIS* (Bonpl.) Cogn. Several varieties of this widely distributed species have been distinguished, most of which seem to depend chiefly on eccentricities in habit alone. Our series of specimens from Colombia includes two forms which differ not only in habit, but also in the structure of the anther. In *Rusby & Pennell 1051*, collected east of Neiva, Dept. Huila, even the lowest cymes are on peduncles less than 1 cm. long, the upper cymes are closely approximate, and the pubescence of the leaves and stem is unusually long. The connective of the anther is not prolonged, but bears two minute gibbosities on the posterior side and a bilobed anterior appendage. The end of the filament is directly under the base of the anther. In our other specimens, the lower cymes are borne on conspicuous peduncles, the upper cymes are well separated, and the pubescence is less conspicuous. The connective is prolonged basally for nearly 1 mm. at right angles, and bears the usual 2-lobed anterior appendage and also a 2-lobed posterior, deflexed appendage about 0.2 mm. long. The end of the filament is quite out of line with the anther.

**Tibouchina lepidota intermedia** n. var. Leaves ovate-elliptic, 8-10 cm. long, 4-4.5 cm. wide, strongly bullate-muricate on the upper surface, beneath foveolate, densely paleaceous on the veins, pubescent on the surface.

Type, *Jameson 87*, from the forests of the Andes, Ecuador, in the temperate montane zone, deposited in the herbarium of the New York Botanical Garden. It is intermediate between the well-known *T. lepidota* (Bonpl.) Baill. and *T. paleacea* (Triana) Cogn., combining the calyx and leaf-shape of the former with the leaf-surface of the latter.

**Ernestia lata** n. sp. Herbaceous or suffrutescent, 5-7 dm. tall; stems erect, simple to the inflorescence, obscurely 4-angled, finely striate, reddish-brown, prominently glandular-villous, densely setose at the nodes; petioles slender, 5-10 mm. long, glandular-villous; leaf-blades firm, ovate-oblong, 35-50 mm. long, 16-28 mm. wide, acuminate, sharply and irregularly serrate with salient, villous and glandular teeth 0.5 mm. long, rounded or truncate at base, upper surface pilose with brown hairs about 1 mm. long, lower surface softly villous, especially on the veinlets, and pilose on the principal veins, 5-nerved, with an obscure outer additional pair, only the midvein impressed above, the veinlets reticulate beneath; upper leaves gradually reduced in size; inflorescence a terminal, nearly leafless panicle 1-2 dm. long, with slender, spreading branches, glandular-villous like the stem; bracts linear-subulate, 2-5 mm. long; pedicels mostly 2-5 mm. long; hypanthium broadly campanulate, 2.7 mm. long by 2.5 mm. in diameter, obscurely 4-ribbed, glandular-villous with spreading hairs 1 mm. long; calyx prolonged 0.3 mm. beyond the staminal torus; sepals triangular-subulate, 4.5 mm. long, acuminate to an aristate tip, entire, widened at the base and meeting in broadly rounded sinuses, the total width 2 mm., sparsely glandular-villous, 3-nerved; petals 4, broadly round-ovate, 6 mm. long, 5 mm. wide, obtuse, truncate at base, glabrous, sparsely setose-ciliolate at the apex; long stamens 4, opposite the sepals: anthers lance-subulate, 2.7-3 mm. long, 0.6 mm. wide at base, opening by an oblique introrse pore; connective slender, thickened below the anther and prolonged 2 mm.; anterior appendage reverse-triangular at base, 1.1 mm. long and wide, flat, prolonged into 2 erect, flat, lance-subulate, straight or flexuous, sparsely serrulate spurs 2.5 mm. long, 0.4 mm. wide at base, separated by a truncate sinus; posterior appendage a minute conic apiculum 0.1 mm. long; filaments brown, flat, straight, 2.0 mm. long, 0.4 mm. wide; short stamens 4, opposite the petals: anthers 2.7 mm. long; connective prolonged 1 mm. at base; anterior appendage narrowly triangular at base, prolonged into 2 linear-subulate, flat, contiguous spurs

3.3 mm. long; posterior appendage conic, 0.2 mm. long; filaments 1.6 mm. long; ovary ovoid-globose, sparsely setose on the upper half and densely glandular-setose at the summit; style filiform, 5 mm. long; stigma minute, capitate. FIG. 2, B.

Type collected by *Weiss & Schmidt*, without number, on the upper Rio Negro, Brazil, 1907-1908, and deposited in the herbarium of the New York Botanical Garden. The measurements of the floral organs are taken from a flower not yet expanded, and the stamens may be considerably longer at anthesis. *E. lata* is a member of the section *Euernestia*, as shown by its setose ovary, and is most closely related to *E. tenella* DC., which was collected in the same general region by Bonpland and by Spruce. *E. tenella* is distinguished from our species by narrower, sparingly serrate leaves, glandular on both sides and on longer petioles, longer pedicels, glabrous petals cuneate to the base, longer connectives, and different appendages.

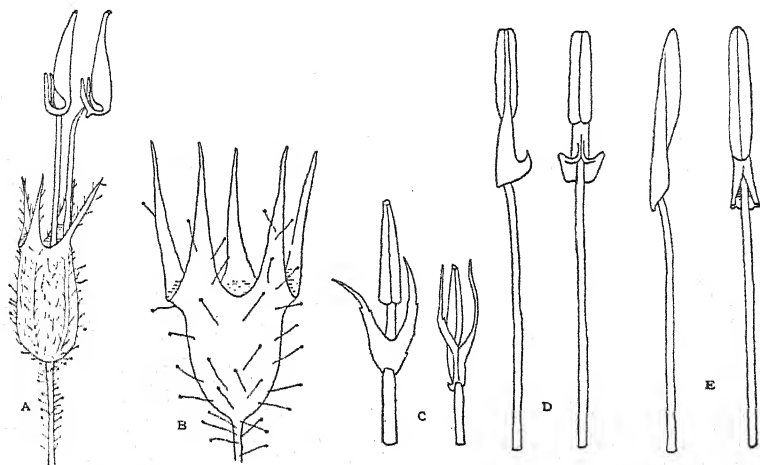


FIG. 2. A. *Ernestia glandulosa* Gleason. B. *Ernestia lata* Gleason, hypanthium; C. stamens. D, E. *Copedesma nitens* Gleason.  $\times 5$ .

***Ernestia glandulosa* n. sp.** Stem herbaceous, 6 dm. high, simple or nearly so, obscurely 4-angled, densely glandular-villous with purple-red hairs when young, becoming sparsely glandular in age, the internodes 3-7 cm. long; leaves of each pair similar; petioles slender, 15-25 mm. long, glandular-villous like the stem; leaf-blades thin and membranous, ovate-oblong, 50-85 mm. long, 20-35 mm. wide, long-acuminate, finely and sharply denticulate (teeth ascending, triangular, 0.2-0.6 mm. long,



about 15 per cm. of margin), rounded or subcordate at base, glandular-villous near the margin, upper surface dark green, villous with ascending hairs about 1 mm. long, lower surface dull green, pubescent with hairs about 0.5 mm. long and purple-villous along the veins, 7-nerved, the veinlets obscure, crooked; racemes 1-3-flowered, axillary, 1-2 cm. long; rhachis and pedicels glandular-villous, bracts subulate, 1 mm. long, setose-tipped; pedicels 3 mm. long, or 8 mm. long in fruit; flowers 4-merous; hypanthium ellipsoid, 3 mm. long, obscurely 8-ribbed, green, glandular-villous; sepals subulate, 2 mm. long, erect, persistent, ciliate and sparsely glandular-villous; petals apparently white, about 8 mm. long, glabrous; stamens similar in size but dimorphic; anthers linear-subulate, 2.8 mm. long, 0.5 wide at base, somewhat recurved at the apex, opening by a minute terminal pore; connective prolonged below the anther toward the anterior side for 0.5-0.7 mm. and terminated by 2 erect, filiform appendages 0.8-0.9 mm. long and nearly parallel to the anther; in 4 stamens the filament is articulated at the anterior end of the connective below a short, conic, descending, posterior appendage 0.2-0.3 mm. long; in the other 4 stamens the filament is articulated at the center of the connective, posterior spur none; filaments almost transparent, slender, flat, 3.8 mm. long, 0.2 mm. wide; ovary globose, free, trilocular, glabrous; style slender, 5 mm. long, straight, terete; stigma punctiform; fruiting hypanthium 4 mm. long; fruit capsular; seeds brown, 0.5 mm. long, obliquely ellipsoid from a truncate base, minutely tuberculate. FIG. 2, A.

Type, *Hitchcock 17,372*, collected along a stream in the forest, Tumatumari, British Guiana, 3-5 Jan. 1920, and deposited in the herbarium of the New York Botanical Garden.

The section *Pseudoernestia* of the genus *Ernestia* was differentiated by Cogniaux because of its 5-merous flowers and glabrous, 3-locular ovary, in contrast to the 4-merous flowers and setose, 4-locular ovary of the section *Euernestia*. Krasser, in the *Natürlichen Pflanzenfamilien*, raised *Pseudoernestia* to generic rank, chiefly, apparently, because of its glabrous ovary. *E. cordifolia* O. Berg., the only species of the section, is known, so far as I can discover, only by a single collection of Spruce on the Orinoco River. Our species differs from it in its small axillary racemes, narrower leaves, and 5-merous flowers. Since it combines the ovary of *Pseudoernestia* with the 5-merous flowers of *Euernestia*, it seems highly doubtful whether Krasser's separation is justifiable, and I have described it under the broader genus *Ernestia*.

*Copedesma*, n. gen.

Flowers 5-merous; hypanthium obconic; sepals broadly triangular, short, the exterior teeth none; petals obovate-oblong, rounded at the apex, glabrous; stamens dimorphic, uniform in size; anthers narrowly linear, opening by a minute terminal pore; filaments elongate, filiform, glabrous; connective much prolonged below the base of the anther-sacs, in some stamens widened posteriorly beyond the attachment of the filament into a flattened, truncate appendage, not appendaged anteriorly, in the others expanded anteriorly at the insertion of the filament into two broad, blunt, triangular, laterally spreading appendages, continuous around the apex of the filament into the broad, truncate, posterior appendage; ovary glabrous, radially ribbed; style filiform, elongate, glabrous; stigma capitate. Woody plants with dark green, glossy foliage, furfuraceous stems, and terminal, slender, stellate-tomentose panicles.

*Copedesma nitens* n. sp. Stems 12 dm. high, branched above, the branches terete or nearly so, closely furfuraceous-tomentulose, glabrescent with age; petioles slender, 10-18 mm. long, pubescent like the stems; leaf-blades membranous, oblong-elliptic, 9-14 cm. long, 3-5.5 cm. wide, long-acuminate to a blunt tip, entire, gradually narrowed from the middle to an obtuse or rounded base, dark-green, shining, and glabrous above, dull green beneath, densely tomentulose on the midvein, thinly furfuraceous on the lateral veins and veinlets, and very sparsely and minutely stellate on the surface, 5-nerved, the outer pair relatively obscure; veinlets about 5 mm. apart, all distinctly impressed above, elevated beneath; panicles slender, 7 cm. long, the branches remote, 5-10 mm. long; bracts linear-spatulate, stellate-tomentose, equaling the hypanthium; flowers sessile; hypanthium 3.2 mm. long, 3 mm. in diameter, densely and closely stellate-tomentose; sepals broadly triangular, 0.6 mm. long, strongly thickened in the center; petals obovate-oblong, white, 2.8 mm. long, 1.7 mm. wide; anther-sacs 2.1-2.4 mm. long; connective prolonged about 1 mm. below the sacs, stout and thick, gradually widened posteriorly to a truncate appendage 1.5 mm. wide, in some stamens bearing also two anterior, broadly conic, laterally spreading appendages, together 1 mm. wide; filaments very slender, glabrous, 4.7 mm. long; style 7.5 mm. long; stigma 0.5 mm. in diameter. FIG. 2, D, E.

Type, *La Cruz 1235*, collected at Tabla, Pomeroon District, British Guiana, 28 Sept. 1921, and deposited in the herbarium of the New York Botanical Garden. Other specimens of the same collection are in the Gray Herbarium, the National Herbarium, and the Philadelphia Academy of Sciences.

This remarkable plant, which unfortunately presents but few open flowers and no fruits, bears a strong superficial resemblance to *Miconia*, but the character of the stamens indicates at once that it is far removed from that genus, and probably in the general affinity of *Ernestia*, of the tribe Tibouchineae. Unlike most genera of that tribe, the anther-sacs, connective, and filament lie in the same line, the connective is unusually stout, in diameter equaling the anther-sacs and considerably exceeding the filament, and the stout appendages are not prolonged into a filiform spur. The general arrangement of these parts is shown far better by the accompanying figures than by description. In the absence of fruit and seeds, its tribal position must remain open to question, but a comparison with the numerous figures of other genera in Triana's monograph or in the *Flora Brasiliensis* will show its fundamental similarity to the Tibouchineae in anther-structure. The anthers are fragile and easily detached from the filaments: in each of the two flowers dissected most of the anthers were missing. It is probable that there are five of each kind, but that could not be confirmed, since the filaments are uniform and it can only be said that both kinds exist in each flower. The generic name is from two Greek roots signifying *sword-hilt* and *connective*.

*Acisanthera glomerata* n. sp. Herbaceous or suffruticose, probably decumbent at base; stems freely branched, sharply quadrangular or narrowly alate, glandular-villous with hairs about 0.5 mm. long; leaves sessile, obovate-spatulate, 7-20 mm. long, 3-6 mm. wide, obtuse, entire or rarely obscurely serrulate, cuneate from above the middle to the base, minutely hirtellous on both sides, glandular-ciliate, obscurely 3-nerved; cymes numerous, terminating the stem and branches, on peduncles 8-15 mm. long; bracts and bractlets sessile, broadly obovate, 4-8 mm. long, obtuse, prominently serrulate toward the apex, pubescent like the leaves; pedicels 1 mm. long or less; flowers 4-merous; hypanthium short-cylindric, 2.8 mm. long, conspicuously 8-nerved, glandular-villous; sepals erect, persistent, membranous, triangular, 3.7 mm. long, 2.5 mm. wide at the base, sharply acute and tipped with a glandular seta, sparsely glandular-villous, prominently 3-nerved and reticulately veined; large stamens 4: anthers oblong, straight, 1.5 mm. long, terminated by a straight, slender, terete rostrum 0.8 mm. long, opening by an introrse terminal pore; connective slender, prolonged 1 mm. at base, sharply introrse for 0.5 mm., and ending in 2 anterior, erect, filiform appendages 1 mm. long, the posterior

side entire or minutely gibbous; filaments flattened, filiform, 2.8 mm. long; small stamens 4: anthers oblong, 1.1 mm. long, terminated by a slender rostrum 0.4 mm. long, the connective prolonged at base 0.4 mm., straight, not appendaged, the filaments slender, 2.8 mm. long; ovary broadly ellipsoid, glabrous, minutely 4-lobed at the summit, 4-locular; style filiform, 4 mm. long, the minute stigma capitate; fruiting hypanthium 3 mm. long; capsule 2-valved, 4-locular, glabrous; seeds brown, 0.5 mm. long, cochleate. FIG. 3, A.

Type, *Samuels 424*, collected in the Forest of Zandery, near Parimaribo, Surinam, 3 July 1916, and deposited in the herbarium of the New York Botanical Garden. Although it has the quadrilocular ovary of Cogniaux's section *Dichaetandra*, it seems to be more closely related in structure and habit to *A. Eoisseriana* Cogn. and *A. hedyotideae* (Presl.) Triana, which have a bilocular ovary, shorter styles, ovate leaves, and shorter sepals separated by conspicuous setae in the sinuses.

***Monochaetum rotundifolium*** Cogniaux, n. sp. Stem shrubby, about 1 m. high, freely branched above, prominently 4-angled, densely pubescent or subtomentose with straight, brown, plumose hairs 0.3-0.5 mm. long; petioles stout, spreading, pubescent like the stem; leaf-blades firm, broadly ovate to subrotund, entire, prominently ciliate, subacute, rounded or somewhat emarginate at base, 7-9-plei-nerved, the outer pair of veins always obscure, upper surface dull green, densely strigose with stout, somewhat plumose hairs papillose at base, lower surface densely and softly pubescent with brown plumose hairs along the veins and gray hairs on the surface; flowers 4-merous, in terminal cymules of 3-7, the peduncles 5-10 mm. long, pubescent like the stem, the pedicels 3-6 mm. long, purple, the pubescence more appressed, decreasing distally, and somewhat glandular; hypanthium purple, ellipsoid-campanulate, 5 mm. long, sparsely appressed-strigose and glandular, pilose at the summit, especially at the sepal sinuses; sepals ovate-triangular, 3.5 mm. long, acuminate, sparsely setulose, minutely ciliate; petals broadly elliptic, apparently about 10 mm. long, ciliate; large anthers lance-subulate, 7 mm. long, conspicuously recurved above the middle, opening by a single terminal dorsal pore, on filaments 6 mm. long, the posterior appendage 2.2 mm. long, expanded above into a broadly lanceolate, somewhat dilated tip; small anthers linear-subulate, 4.5 mm. long, nearly straight, on filaments 7 mm. long, the appendage flat, elliptic-lanceolate, 2 mm. long; ovary nearly free, obscurely 4-angled, pubescent above, minutely 4-lobed and setose at the summit; style slender, 9 mm. long, decurved near the apex; stigma punctiform. FIG. 3, D.

This remarkable plant, which unfortunately presents but few open flowers and no fruits, bears a strong superficial resemblance to *Miconia*, but the character of the stamens indicates at once that it is far removed from that genus, and probably in the general affinity of *Ernestia*, of the tribe Tibouchineae. Unlike most genera of that tribe, the anther-sacs, connective, and filament lie in the same line, the connective is unusually stout, in diameter equaling the anther-sacs and considerably exceeding the filament, and the stout appendages are not prolonged into a filiform spur. The general arrangement of these parts is shown far better by the accompanying figures than by description. In the absence of fruit and seeds, its tribal position must remain open to question, but a comparison with the numerous figures of other genera in Triana's monograph or in the *Flora Brasiliensis* will show its fundamental similarity to the Tibouchineae in anther-structure. The anthers are fragile and easily detached from the filaments: in each of the two flowers dissected most of the anthers were missing. It is probable that there are five of each kind, but that could not be confirmed, since the filaments are uniform and it can only be said that both kinds exist in each flower. The generic name is from two Greek roots signifying *sword-hilt* and *connective*.

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side entire or minutely gibbous; filaments flattened, filiform, 2.8 mm. long; small stamens 4: anthers oblong, 1.1 mm. long, terminated by a slender rostrum 0.4 mm. long, the connective prolonged at base 0.4 mm., straight, not appendaged, the filaments slender, 2.8 mm. long; ovary broadly ellipsoid, glabrous, minutely 4-lobed at the summit, 4-locular; style filiform, 4 mm. long, the minute stigma capitate; fruiting hypanthium 3 mm. long; capsule 2-valved, 4-locular, glabrous; seeds brown, 0.5 mm. long, cochleate. FIG. 3, A.

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***Monochaetum rotundifolium*** Cogniaux, n. sp. Stem shrubby, about 1 m. high, freely branched above, prominently 4-angled, densely pubescent or subtomentose with straight, brown, plumose hairs 0.3–0.5 mm. long; petioles stout, spreading, pubescent like the stem; leaf-blades firm, broadly ovate to subrotund, entire, prominently ciliate, subacute, rounded or somewhat emarginate at base, 7–9-plexi-nerved, the outer pair of veins always obscure, upper surface dull green, densely strigose with stout, somewhat plumose hairs papillose at base, lower surface densely and softly pubescent with brown plumose hairs along the veins and gray hairs on the surface; flowers 4-merous, in terminal cymules of 3–7, the peduncles 5–10 mm. long, pubescent like the stem, the pedicels 3–6 mm. long, purple, the pubescence more appressed, decreasing distally, and somewhat glandular; hypanthium purple, ellipsoid-campanulate, 5 mm. long, sparsely appressed-strigose and glandular, pilose at the summit, especially at the sepalar sinuses; sepals ovate-triangular, 3.5 mm. long, acuminate, sparsely setulose, minutely ciliate; petals broadly elliptic, apparently about 10 mm. long, ciliate; large anthers lance-subulate, 7 mm. long, conspicuously recurved above the middle, opening by a single terminal dorsal pore, on filaments 6 mm. long, the posterior appendage 2.2 mm. long, expanded above into a broadly lanceolate, somewhat dilated tip; small anthers linear-subulate, 4.5 mm. long, nearly straight, on filaments 7 mm. long, the appendage flat, elliptic-lanceolate, 2 mm. long; ovary nearly free, obscurely 4-angled, pubescent above, minutely 4-lobed and setose at the summit; style slender, 9 mm. long, decurved near the apex; stigma punctiform. FIG. 3, D.

Type, *Smith 1851*, collected on San Lorenzo Ridge, Santa Marta, Colombia, alt. 6000-7000 ft., 27 Feb. 1899, and deposited in the herbarium of the New York Botanical Garden. The sheet exhibits two specimens, differing only in the size of the leaves, and is accompanied by the collector's note: "A shrub 3-4 ft. Common on open ridges, 6000-7500 ft. Below 6500 ft. the leaves are larger, but the plants do not otherwise differ. Flowers observed Jan.-March. Petals rosy. The specimens are from the San Lorenzo Ridge, Feb. 27; the small-leaved one collected at about 7000 ft., the other at about 6000 ft." On the large-leaved plant, the length of the petiole is fairly uniform at 7-9 mm.; the size of the blade varies from 30 by 24 mm. for the largest to 10 by 8 mm. for those subtending the cymules. On the small-leaved specimen, which is to be considered the type, should differentiation be necessary, the petioles rarely exceed 5 mm. and the blades vary from 15 by 11 mm. down to 7 by 5 mm.

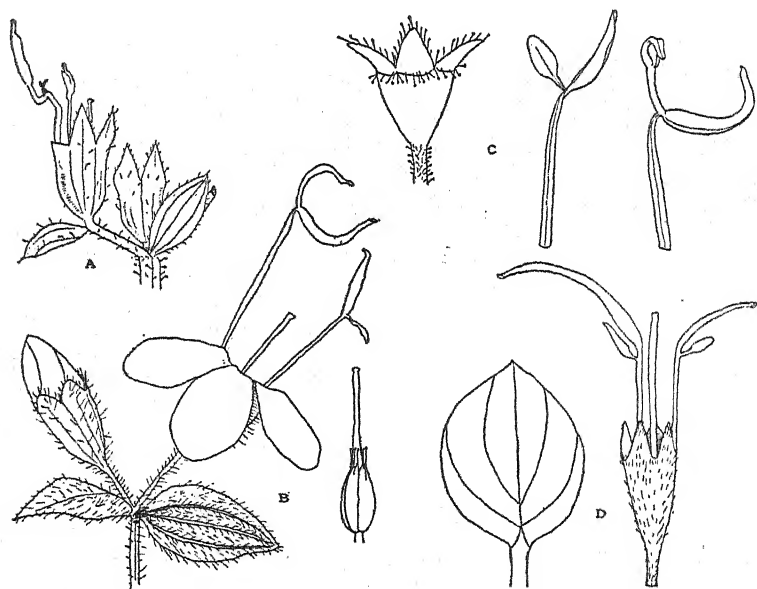


FIG. 3. A. *Acisanthera glomerata* Gleason,  $\times 2.5$ . B. *Monochaetum villosum* Gleason,  $\times 2$ ; ovary and style,  $\times 2$ . C. *Monochaetum coronatum* Gleason, hypanthium and stamens,  $\times 2.5$ . D. *Monochaetum rotundifolium* Cogn.,  $\times 2$ .

Cogniaux, who examined the plant, noted that it represented an undescribed species, suggested the name here used, and indicated its close affinity to *M. stellulatum* Naud. Our species differs in its smaller and proportionately broader leaves, in its much larger anthers with proportionately smaller appendages, its longer sepals, and its colored flowers.

**Monochaetum villosum** n. sp. Stem shrubby, freely branched above, minutely 4-angled, villous with spreading or somewhat deflexed, slender, purple hairs 1.5–2 mm. long, the nodes densely villous; petioles slender, about 5 mm. long, villous like the stem, leaf-blades firm, ovate, entire, subacuminate to an acute apex, rounded or subcordate at base, 5-plexi-nerved, the veins obscure above, somewhat conspicuous beneath, the veinlets obscure, upper surface softly villous with spreading, slender, pale hairs, slightly enlarged toward their base, about 2 mm. long, set about 0.3 mm. apart, lower surface more sparsely villous with similar but shorter hairs; flowers 4-merous, in cymules of 3, or rarely single, terminating the upper branchlets, on pedicels 2–4 mm. long; hypanthium purplish-green, narrowly campanulate or obconic, 5 mm. long, tapering to the base, faintly 8-ribbed, sparsely villous with straight, slender, spreading purple hairs, about 1 mm. long, set 0.3–0.5 mm. apart, and frequently glandular; sepals membranous, ovate-triangular, 1.8 mm. long and wide, barely acute, sparsely setose on the back like the hypanthium, strongly ciliate with curved hairs 0.8 mm. long; petals white, obovate, 8 mm. long, minutely ciliate; stamens dimorphic; anthers linear-subulate, opening by a single dorsal terminal pore, connective not prolonged anteriorly, prominently appendaged on the posterior side; larger anthers strongly curved, 6.5 mm. long, the appendages 4 mm. long, with 2 longitudinal ridges at the base and 3 at the somewhat expanded apex, the filaments 5.7 mm. long, flat, 0.7 mm. wide at base, tapering slightly to the summit; smaller anthers nearly straight, 4.3 mm. long, the appendages strongly flattened, spatulate, 2.7 mm. long, 0.6 mm. wide, the filaments 7.3 mm. long, flattened below, terete above; ovary free, 4-lobed, 4-locular, glabrous below, the summit minutely 4-lobed, each lobe tipped with 2 or 3 glandular setae 0.7–1 mm. long; style glabrous, subulate, declined, 6.5 mm. long; stigma punctiform. FIG. 3, B.

Type, *Rusby & Pennell 804*, collected in forest at "Balsillas," on the Rio Balsillas, Dept. Huila, Colombia, alt. 2100–2200 m., 3–5 Aug. 1917, and deposited in the herbarium of the New York Botanical Garden. The largest leaves are 18–22 mm. long by 11–14 mm. wide; the upper leaves are reduced and those subtending the cymules are barely 5 mm. long. The species is a



member of the section *Eumonochoetum*, with persistent sepals, and is most closely related to the Peruvian *M. dicranantherum* (R. & P.) Naud.

***Monochaetum coronatum*** n. sp. Stem shrubby, freely branched above, obscurely 4-angled, finely and persistently glandular-pubescent with spreading hairs mostly 0.2–0.4 mm. long, densely hirsute at the nodes; petioles stout, 3–5 (rarely 10) mm. long, densely glandular-hirsute; leaf-blades thin, broadly ovate, entire, glandular-ciliate, broadly acute, rounded at the base, 5–7-plei-nerved, upper surface conspicuously but sparsely setose with appressed or ascending, yellowish, non-glandular hairs 0.6–1 mm. long, lower surface softly pubescent with spreading, slender, white hairs; flowers 4-merous, in terminal cymules of 3–5, on densely glandular pedicels 3–7 mm. long; hypanthium purplish, campanulate, 5 mm. long by 3.7 mm. in diameter, obscurely 4-angled, glabrous on the sides, setose at the summit with sparse, erect or ascending, glandular hairs nearly or quite 1 mm. long; sepals triangular, 2.8–3 mm. long, 2.5 mm. wide, acute, sparsely glandular-setose on the back, conspicuously glandular-ciliate, glabrous within; petals white, broadly elliptic, 1 cm. long, obtuse, glabrous, very sparsely glandular-ciliate at the apex; filaments of the large stamens flat, nearly 6 mm. long, of the small stamens similar, 8 mm. long; anthers of the large stamens lance-subulate, 6.3 mm. long, strongly recurved, with a single terminal dorsal pore, the basal posterior appendage 5 mm. long, its basal half stout, 2-ribbed on the dorsal side, the distal half more or less inflated, ovate-lanceolate, blunt, strongly bent or recurved near the apex; anthers of the small stamens linear-subulate, nearly straight, 4.8 mm. long, the appendage flat, 3.3 mm. long, the distal two-thirds expanded into an elliptic obtuse tip 0.8 mm. wide; ovary nearly free, obscurely 4-lobed, minutely 4-lobed at the summit, glabrous; style slender, 7 mm. long, glabrous, decurved near the apex; stigma punctiform. FIG. 3, C.

Type, *Pennell 2449*, collected in a clearing, 2–4 miles south of Sibate, Dept. Cundimarca, Colombia, alt. 2800–2900 m., 13–15 Oct. 1917, and deposited in the herbarium of the New York Botanical Garden. The largest leaves measure 35 by 21 mm., the upper are gradually reduced in size, and those subtending the cymules are only 10–15 mm. long. *M. coronatum* is most closely related to *M. Jahnni* Pittier, a Venezuelan species which also has a glabrous hypanthium surmounted by glandular sepals. Our species differs in its denser glandular pubescence, glandular-ciliate leaves, glandular pedicels, longer, acute sepals, larger, white petals, and much larger anthers.

**Rhynchanthera microphylla** n. sp. Stem shrubby, prominently 4-angled and swollen at the nodes, freely branching above, thinly pubescent above with spreading non-glandular hairs 0.1-0.2 mm. long, becoming glabrate with age, the internodes 1-2 cm. long; petioles flattened, 2-6 mm. long, pubescent like the stem; leaf-blades firm, oblong-ovate, 9-20 mm. long, 5-11 mm. wide, minutely setulose-serrulate, acute, broadly obtuse to subrotund at base, 5-nerved, upper surface thinly strigose with yellow hairs 0.2-0.3 mm. long, the lower thinly pubescent with spreading hairs of the same size; flowers 5-merous, in terminal cymules of 1-3, the villous pedicels 1 mm. long; hypanthium 6 mm. long, cylindric below, expanded toward the summit, pubescent like the stem; sepals linear-subulate, spreading at anthesis, 10 mm. long, thinly pubescent; petals bright magenta, 2 cm. long; fertile stamens 5, equal, the anthers lance-subulate, prolonged into a flattened, slightly curved beak with a single apical pore, the connective prolonged at base and minutely bituberculate on the anterior side; sterile stamens reduced to linear-filiform sterile filaments; ovary free, glabrous; style nearly straight, the stigma minutely capitate.

Type, *Hitchcock 16,985*, collected on the East Coast Water Conservancy, southeast of Georgetown, British Guiana, about sea-level, 27 Nov. 1919, and deposited in the herbarium of the New York Botanical Garden. The necessary dissections from which the description was drawn were made from a bud, in which the anthers were 5 mm. long, including the beak of 1.1 mm. Obviously a member of the section *Isostemones*, our species appears most closely related to the last three species of Cogniaux's monograph, and differs from *R. Glazioviana* Cogn. and *R. serrulata* (Rich.) DC. in its broader leaves, and from *R. parviflora* Cogn. in its smaller leaves and much larger flowers.

**Siphanthera alsinoides** n. sp. Annual, 10-15 cm. high; stems herbaceous, sharply 4-angled or narrowly 4-winged, slender, sparsely hispidulous and glandular-villous, the internodes 18-40 mm. long; petioles flattened, 1-3 mm. long, pubescent like the stem; leaf-blades thin, broadly ovate, 5-9 mm. long, 5-7 mm. wide, obtuse or subacute, crenate-serrulate, especially distally, rounded or subcordate at base, sparsely hispid above with stout, subulate, somewhat paleaceous hairs 0.6-1 mm. long, beneath pale green, glabrous on the surface, minutely and sparsely villous on the veins, obscurely 3-nerved; inflorescence a terminal, sympodial, bracted cyme, each axis ending in a flower subtended by 2 bracts, from the axils of which secondary axes arise, 2-4 cm. long; bracts ovate, sessile, acute, 2-3 mm. long; pedicels sharply 4-angled, 0.7 mm. long; flowers 4-merous;

hypanthium oblong-campanulate, 1.8 mm. long, 1.1 mm. in diameter, pale brown, almost scarious, obscurely 8-nerved, sparsely glandular-villous with hairs 0.4 mm. long; sepals scarious, triangular, 1.5 mm. long by half as wide at the base, sharply acute, reticulate-veined, glabrate; petals rose-pink, apparently fugacious, 3 mm. long, obovate, narrowed to the base, glabrous; stamens 8, dimorphic; fertile stamens: anthers broadly oblong, 0.7 mm. long, 0.5 mm. wide, deep violet, rounded at both ends, glabrous, the rostrum pale violet, terete, 0.2 mm. long and in diameter, obliquely truncate with an introrse pore; connective slender, violet, the basal prolongation 0.3 mm. long, yellow, expanded at the apex into 2 anterior, semicircular appendages, 0.2 mm. long and a little wider; filaments violet-brown, very slender, 1.8-2 mm. long; sterile stamens: anthers yellow, linear-fusiform, 0.3 mm. long; connective not prolonged; filaments 1.6 mm. long; ovary free, ellipsoid, 1 mm. long, glabrous, 2-locular; style straight, 3.7 mm. long, 0.1 mm. in diameter, minutely fusiform-dilated near the apex; stigma spherical, 0.2 mm. in diameter; fruiting hypanthium 3 mm. long, prominently nerved; capsule oblong-cylindric, 2.5 mm. long, depressed at the apex, glabrous, loculicidal; seeds ellipsoid, 0.5 mm. long. FIG. 4, A.

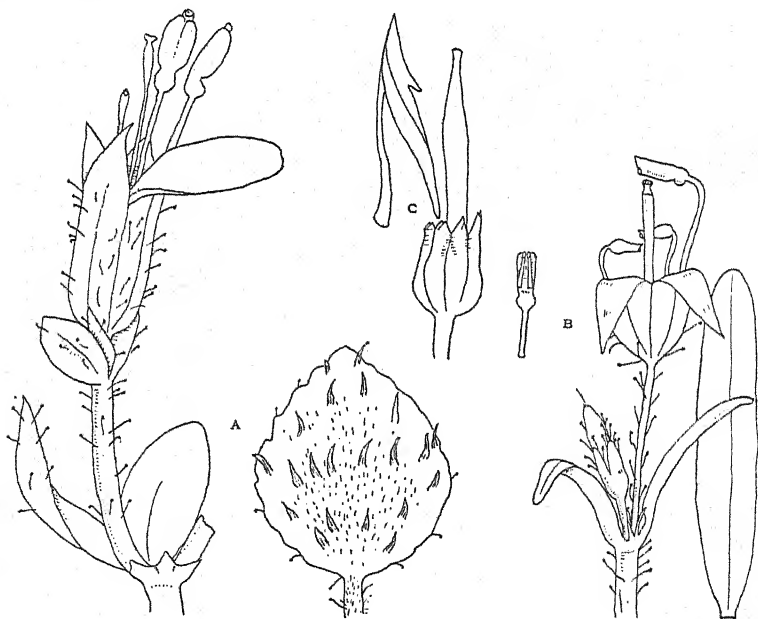


FIG. 4. A. *Siphantha alsinoides* Gleason, with foliage leaf,  $\times 7.5$ . B. *Poteranthera minor* Gleason, flower, leaf, and anterior face of anther,  $\times 7.5$ . C. *Centronia mutabilis* Gleason, pistil and detached stamen,  $\times 2$ .

Type, *Pennell 1467*, collected in a moist depression in the llano east of Villavicencio, Intendencia Meta, Colombia, alt. 450 m., 26-31 Aug. 1917, and deposited on the herbarium of the New York Botanical Garden. The color of the anthers is taken from the dried specimen: the collector noted them as pink-purple, white at the base.

Since Cogniaux' treatment of *Siphanthera* in his monograph over twenty years ago, no additional species has been described, nor have any been reported from as far west as Colombia. Our plant presents precisely the staminal structure of the genus as hitherto known, but differs from the other species in its cymose inflorescence.

***Poteranthera minor* n. sp.** Herbaceous annual, 5-10 cm. tall, simple or sparingly branched; stems sharply 4-angled, glabrate below, sparsely hispidulous and glandular-villous above, increasing toward the apex, the upper internodes 1-2 cm. long; leaves sessile, crowded at the base of the stem, linear, 6-10 mm. long, 1-1.5 mm. wide, the upper smaller and bractlike, acute, rarely spinulose-ciliate, glabrous on both sides, obscurely 1-nerved; flowers solitary in the upper axils and appearing cymose from the shortening of the terminal internodes, 4-merous; bracts resembling the leaves, 3-5 mm. long, somewhat glandular-villous; pedicels 2-3.5 mm. long, densely glandular-villous; hypanthium campanulate, 1.6 mm. long, 1.1 mm. in diameter, sparsely glandular-villous with violet hairs 0.6-0.8 mm. long, 8-nerved; sepals membranous, triangular, 2.5 mm. long, 1 mm. wide at base, acuminate to a subulate tip, very sparsely glandular-villous, obscurely nerved; petals deciduous, pink-purple; fertile stamens 4, alternate with the petals: anthers oblong, thick, 0.6 mm. long by 0.3 mm. wide and thick, the anther-sacs separate below, connivent above, very slender, violet-colored, opening each by a terminal pore as wide as the sac; connective thick, gradually widened to the base of the anther, prolonged into a subglobose base 0.4 mm. in diameter and minutely 2-tuberculate anteriorly; filaments straight, filiform, 1.7 mm. long; sterile stamens 4, opposite the petals, the anthers narrowly ovoid, 0.5 mm. long, acuminate, minutely 1-pored, the connective not prolonged, the filaments incurved, filiform, 1.3 mm. long; ovary glabrous, 2-locular, subglobose; style straight, 3 mm. long, filiform, somewhat fusiform-thickened below the summit; stigma capitate, 0.2 mm. in diameter; fruiting hypanthium somewhat expanded, the sepals persistent; capsule 2.5 mm. long, loculicidal. FIG. 4, B.

Type, *Pennell 1423*, collected in a moist depression in prairie,

Villavicencio, Intendencia Meta, Colombia, alt. 450 m., 26-31 Aug. 1917, and deposited in the herbarium of the New York Botanical Garden. It is a member of the section *Tulasnea*, characterized by 4-merous flowers and clavate style, and differs from the two species hitherto known in various structural features and dimensions, but particularly in its strongly thickened anthers.

***Centronia mutabilis* n. sp.** Arborescent; branches, petioles, lower leaf-surface, peduncles, pedicels, and calyx prominently fulvous-furfuraceous; stems obscurely 4-angled, the internodes 1-2 cm. long; petioles stout, straight, 15-20 mm. long; leaf-blades firm or coriaceous, ovate or ovate-oblong, 8-9 cm. long, 4-5 cm. wide, obtuse or abruptly acute, sharply obcrenulate (about 5 teeth per cm. of margin, 0.5-1 mm. high), obtuse to truncate or barely cordulate at base, minutely furfuraceous above when young, dark green and glabrous at maturity, 7-pinnerved, the outer pair obscure and marginal, the transverse veins prominent beneath, about 2 mm. apart, the veinlets minutely reticulate under the lens; leaves of the floriferous branches smaller, 4-6 cm. long, 5-pinnerved; panicles ascending or erect, 8-10 cm. long, about 10-flowered; pedicels stout, 5-9 mm. long; flower-buds 2 cm. long, obovoid, abruptly beaked, the calyx-limb irregularly deciduous about 8 mm. from the base; flowers 6-merous; petals red, changing to blue, obovate-oblong, 25 mm. long, 20 mm. wide, obtuse, minutely carinate at the apex; filaments strongly flattened tangentially, erect, 10 mm. long; anthers subulate, 9 mm. long; the connective prolonged at base into an acute, conical spur 5.5 mm. long, with a much smaller dorsal appendage extending forward; ovary 6 mm. long, the distal half dissected into flat, lance-oblong, setulose lobes with free acuminate tips 1.5 mm. long; style subulate, 12 mm. long. FIG. 4, C.

Type, *Pennell* 9385, collected at "Alaska," above Salento, Dept. Caldas, Colombia, 7 Aug. 1922, alt. 3100-3400 m., and deposited in the herbarium of the New York Botanical Garden. Another collection is *Hazen* 9689, collected at "Cucarronera," New Quindio Trail, Dept. Caldas, 8 Aug. 1922. In superficial appearance and in the structure of the anther-appendage, the species closely resembles *Centronia haemantha* (Planch. & Lind.) Triana, as illustrated in *Flore des Serres*, plate 924, and in *Trans. Linn. Soc.* 28: *pl.* 5, *fig.* 59b. But the structure of the ovary is distinctly that of a different section of the genus, *Centroniotypus*. Here it finds its nearest relative in *Centronia Mutisii* (Bonpl.) Triana, also from the Quindio region, which differs in its hispid pubescence, larger leaves, longer pedicels, and white petals.

# INDEX TO AMERICAN BOTANICAL LITERATURE

1911-1925

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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The effect of wounds upon the rotation of the protoplasm in  
the internodes of *Nitella*

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(WITH FOUR TEXT FIGURES)

The cause of traumatic shock has been the subject of many investigations in recent years, especially in the animal kingdom (Cannon 2, Crile 4, Mann 14, Seifriz 17), although plants have received some attention (Bayliss 1, Fitting 6, Lillie 13). The theories advanced in explanation are somewhat confusing and contradictory.

While studying the process of healing in plant cells, it was observed that the internodal cells of *Nitella* offered an unusual opportunity to study the reactions of streaming protoplasm to wounds. Therefore a series of experiments was carried out in the hope of gaining further evidence as to the traumatic response of active cells and, if possible, the nature of traumatic shock.

That protoplasm will recover from mechanical injury and later show streaming has been demonstrated many times. Hofer (9) sectioned *Amoeba* and found that streaming was recovered in the fragments although the nucleus might not be present in the isolated portion. Hertwig (8) and Verworn (18) sectioned swarmspores and infusoria and found that the ciliated portions regained their movement while non-ciliated sections remained quiet. Hauptfleisch (12), Pfeffer (15), Gerassinoff (7), and Hofmeister (10), have obtained similar results in plant cells. By plasmolysis or induction shocks they isolated in the cell non-nucleated portions in which streaming was maintained for several hours.

A portion of the plant two or three internodes long is mounted in a drop of water and under a low power objective punctured,

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free-hand, with a steel needle ground to a very fine point. The effect upon the protoplasm, which I wish to report, is indicated by the change in the rate of movement shown by the particles carried in the streaming protoplasm. The rate is obtained by taking on a stop-watch the time that a grain requires to move five units, equal to 80 microns as measured by the ocular micrometer. The term "normal rate" is used in referring to the average rate at which the protoplasm is moving in the unpunctured cells of the control. The control is a specimen consisting of the same number of internodes, usually three, as nearly as possible of the same age, size and condition as the material under experimentation. Before beginning an experiment a specimen is selected in which the protoplasm is moving at the same rate as that in the cells of the control. The experiment and control material were both handled in the same way and both remained under the same cultural conditions.

As the needle passes through the wall a number of plastids are torn loose, leaving a clear area around the opening. On the withdrawal of the needle from the hole a certain amount of protoplasm with its plastids, starch-grains, and other particles pours out into the surrounding water. The protoplasm is not at once miscible but forms globular masses just outside of the opening. After a minute or two granules begin to accumulate in the opening. This mass seems to harden, forming a plug, and the loss of protoplasm ceases. Gradually a new membrane forms inside of the cell wall separating the plug from the remainder of the protoplasm. The new membrane soon begins to form a new wall and the healing is complete.

By maintaining a clear focus on the point of the needle as it passes through the wall it is possible to observe an immediate retardation or cessation of the streaming movement, which may be general throughout the cell, or be limited to a region near the wound. The effect of the puncture upon the rotation of the protoplasm is influenced by the sharpness of the needle, location of the puncture in the internode, the number of times the internode has been punctured, as well as the size and depth of the wound.

The first puncture of an internodal cell more frequently causes all movement to cease than later punctures made the same day. If the cell is punctured repeatedly for several days,

the first puncture of each day is more apt to cause cessation than later punctures.

The cell wall is very pliable and gives readily before the needle, but if the needle is so sharp that it passes through the wall with very slight bending at the point of contact it forms a puncture that does not cause the movement to cease throughout the cell, but only in a section near the wound. The portion of the protoplasm affected varies according to the character of the wound. When the wound is large (100-200 microns) and followed by a correspondingly large loss of protoplasm, there may be a pronounced retardation throughout the cell, but frequently one end or both will show granules moving at the normal rate. If the puncture is not so large (60-100 microns) movement may be present in the major portion of the cell while the protoplasm is escaping through the partially plugged opening.

When a sharp needle is passed through the wall slowly many of the particles in the field of vision show only a slight, if any, retardation. Just at the time of puncturing some of the granules in the course of the flowing protoplasm both above and below the wound, cease to move, while laterally there are grains that do not show any effect.

A wound of the same size, but made with a quick thrust, always results in a more pronounced reaction as shown by the increased area affected, as well as the longer period required for recovery. That the amount of injury suffered by the protoplasm is dependent on the way the needle is handled has been observed by Chambers (3) and Seifriz (17). Chambers states that "one may puncture a cell with a needle and drag the needle back and forth cutting through the cell, and if the procedure be slow and gradual the tear closes up behind as the needle proceeds and the process may be continued almost 'ad libitum' without producing any ill effect. If, on the other hand, the needle is carried rapidly through the cytoplasm, a few thrusts only are necessary to induce rapid disorganization."

The difficulty of piercing the wall may account for the fact that the most carefully made puncture of a *Nitella* cell is always followed by a definite injury resulting in some retardation for 2-5 minutes at least in the protoplasm passing the wound.

When the needle is slightly dull the wall bends at the point of pressure, and as the needle penetrates, the wall springs back into position, causing a slight jar or vibration to pass through the cell. This action is accompanied by an immediate cessation of movement throughout the cell. Complete cessation of movement throughout was never observed except when it could be accounted for either by the readjustment of the wall or an explosive loss of protoplasm following the puncture. That a jar or any mechanical shock which may start a vibration will cause cessation throughout a streaming cell has been observed and discussed so many times that it does not require further comment at this time (Ewart 5, Hörmann 11, Hauptfleisch 12, Pfeffer 15).

Movement is not resumed simultaneously throughout the cell, but here and there a granule will be observed to move slowly (20-30 seconds per 80 microns) while the adjacent particles are quiet. The movement spreads rapidly until all the granules are moving except in a region near the wound. Hörmann (11) observed that the internodal cell in *Nitella* might show more than one rate of movement under experimental conditions. When he immersed one end of a cell in water and the other in a sugar solution, a decrease in the velocity of movement in the end immersed in the sugar solution was observed. Hörmann thought that this effect was the result of the stimulating action of the sugar solution upon the protoplasm. Ewart (5) repeated the experiment and decided that the sugar solution did not act as a stimulus, but through ex-osmosis increased the viscosity of the protoplasm and therefore decreased the velocity of movement.

Recovery in the region near the wound follows the same general course in every case, whether it has been preceded by a general cessation of movement, or only by the formation of a quiet area at the puncture. I will describe one of my experiments in detail in order to outline this process.

An internode 2.5 cm. long and 1.5 mm. wide was mounted and punctured one cm. from the end. The puncture was about midway between the two neutral zones. A quick thrust with a sharp needle formed a puncture 105 microns by 45 microns. The plug formed without excessive loss of protoplasm. At the time of puncturing there was a very slight retardation through-

out the cell and complete cessation of movement in the particles moving toward, and by the wound, for a distance of 160 microns. Some of the particles in the current moving away from the wound ceased to move immediately while others continued to move very slowly (52 seconds per 80 microns). As an immediate result of the wounding in this case, in the region below the puncture and along the lines of flowing protoplasm there were fewer granules visible than in the remainder of the internode. This may be because it is the motion which enables one to see certain of these particles whose optical properties are not very different from those of the mass in which they are imbedded. After one to two minutes there was no visible movement in this area, which could be traced for 1280 microns before it passed out of view around the side of the internode.

The first movement in the quiet area was shown by granules passing the wound laterally. After the first slow movement the rate increased very rapidly until they were moving normally. During the first two or three minutes there was a very slight retardation just as they passed the wound.

After a brief interval (30 seconds) the granules in the line of previous flow and in the direction from which the cytoplasm was coming, were once more carried toward the wound, where their movement was checked. As the granules were checked, some came to rest while others moved laterally and around the wound until they were caught in the adjacent stream of more rapidly moving protoplasm. The movement spread rapidly throughout this region and in a few seconds the whole mass was moving. The rate increased steadily but somewhat more slowly than laterally from the wound, yet in three minutes the whole mass was moving normally.

This checking of the movement in the region of the wound-plug resulted in an accumulation of material just above the wound. This mass soon became so dense that it was impossible to focus on any definite grain to follow its course. Granules were steadily carried out of this mass and borne away in the streaming protoplasm passing the wound laterally. There was the appearance then of two dense masses of moving protoplasm, one extending from each end of the wound.

As the normal rate of streaming was re-established laterally from the wound during the first two seconds, the transition

from the quiet area, down-stream from the wound, to normally flowing cytoplasm was very abrupt. There was a narrow zone about 16 microns wide of slowly moving particles between the two regions. The streaming protoplasm gradually encroached on the quiet area, thus narrowing and shortening the region. This process continued for several minutes. The quiet area was capped and bordered by dense masses of slowly moving protoplasm, while the remainder of the cytoplasm in the internode was moving normally, as shown in FIG. 1.

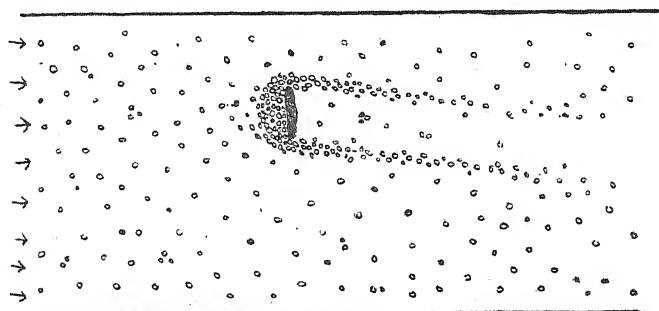


FIG. 1. Diagram illustrating the arrangement of granules at the wound about ten minutes after puncturing.

Finally the mass of material pressing against the wound began to pass under the wound-plug, starting a movement in the quiet area on the other side. The granules were moving slowly as they passed the plug, but did not stop entirely when they came in contact with the quiet protoplasm; instead they were carried laterally until they were caught and carried away in the bordering streams of cytoplasm. This action continued for a minute or two. At this time there is movement between the wound and the quiet area below. Focusing through this area, it was sometimes possible to see particles carried along under it as they were under the wound. After about three minutes the entire region began to show movement slowly (30 seconds per 80 microns). The rate increased very slowly. After four hours there was still a noticeable retardation in this region. This was in marked contrast to the procedure in the other portions of the cell where movement once started, gains its normal rate in a few minutes, as shown in FIGS 2 and 3.

The next morning the entire protoplasm of the cell was rotating normally at 1.5 seconds per 80 microns.

Sometimes in puncturing, the number of plastids loosened from the wall was very large, leaving a correspondingly large clear area around the puncture. When this happened it was easier to follow the movement near the wound. In one such instance, when experimenting on an internode containing only

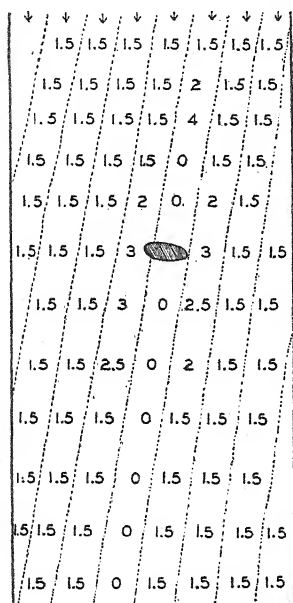


FIG. 2.

FIG. 2. Diagram illustrating the rate at which the granules are carried 30 minutes after puncturing.

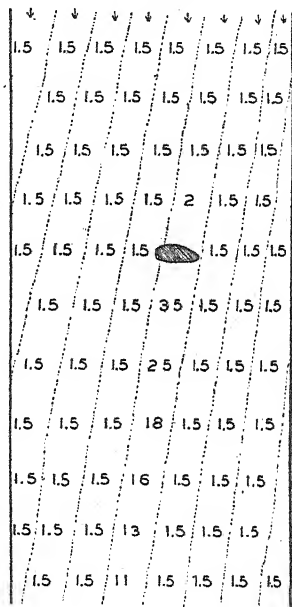


FIG. 3.

FIG. 3. Diagram illustrating the rate at which the granules are carried one hour after puncturing.

The rates shown in the diagrams were obtained by averaging twenty-five experiments. Each numeral indicates the number of seconds taken by a particle in moving 80 microns when in that position in relation to the wound. The granules were timed every alternate 80 microns as long as they were in view.

a few floating particles, it was observed that a mass of dense protoplasm with two or three granules embedded in it was loosened from the wall and carried away in the stream. Apparently this mass formed a portion of the quiet area.

If the puncture is made in the neutral zone the disturbance to the rotation may be very slight. On each side of the zone there is a current toward the wound and the additional quiet

area is correspondingly reduced, facilitating rapid recovery. The final effect is that of a slightly distended neutral zone at this point. Occasionally a very pronounced reaction follows the puncture. As the granules are checked at the wound, some are carried slowly around the wound area, and pass on in their normal direction. Other particles, slightly nearer the neutral zone, are carried toward it, slowly cross the zone and join the stream on the other side, and reverse their direction of flow. This may take place just at the wound, or at some little distance from it (320 microns). It may occur on both sides of the wound, leaving an area across the cell without any visible movement, or one stream only may cross the zone, the other moving by the

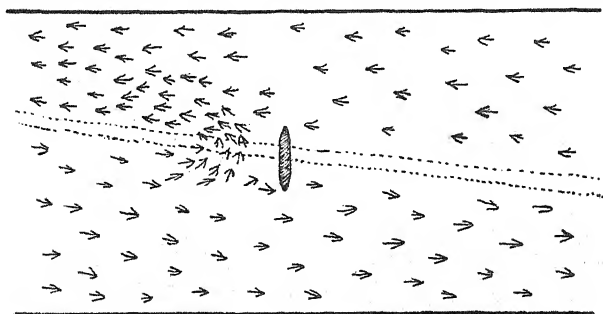


FIG. 4. Diagram illustrating the movement of the granules in some cases when the internode is punctured in the neutral zone.

wound in the normal manner. When this last condition results, the number of granules in one end of the cell increases steadily, while the number in the other decreases, resulting in a very uneven distribution of the material. Slowly the number crossing the neutral zone decreases, while more and more pass around and under the wound until the normal rotation is re-established (FIG. 4).

Repeated puncturing of the cell, without waiting for the resumption of movement in the protoplasm passing under the wound, results in a more pronounced reaction by the protoplasm. After the third or fourth puncture, recovery is noticeably slower although the general course is the same as after the first puncture. The following table is made from a series of experiments in which the cell was punctured as soon as there was any visible movement, the puncture being made in the section

of the cell where the movement occurred. Each experiment was considered closed when no further movement was observed on the day of the experiment. In every case the normal rate (2 seconds per 80 microns) was present in the cell when examined the next morning.

TABLE SHOWING THE TIME BETWEEN PUNCTURING AND THE FIRST VISIBLE MOVEMENT IN ANY PART OF THE CELL.

No. of the puncture	Exper. 1	Exper. 2	Exper. 3
1	0	30 sec.	0
2	0	0	0
3	1 min.	2 min.	30 sec.
4	2 "	6 "	1 min.
5	4 "	10 "	7 "
6	4 "	11 "	9 "
7	10 "	15 "	10 "
8	12 "	16 "	14 "
9	20 "	18 "	16 "
10	18 "	25 "	21 "
11	27 "	45 "	30 "
12	42 "	1 hr. 12 min.	50 "
13	1 hr. 27 min.	—————	1 hr. 40 min.
14	3 hrs.	—————	—————

If the second puncture is not made until after the movement has been resumed throughout the cell, although there is retardation of the movement in the protoplasm passing under the wound, the reaction may be less pronounced. The time between the puncture and the resumption of movement is shorter, especially in the cytoplasm moving toward the wound. Each successive puncture is followed by a more rapid resumption of movement. After several punctures (five to eight) the protoplasm does not entirely cease to move toward the puncture although it may be retarded as it approaches the wound. Movement from the wound ceases but is resumed after a short pause (two to four minutes). The tenth or thirteenth puncture may be followed by a pause at the wound while the plug is being formed, movement being resumed as soon as the escape of protoplasm ceases. The granules begin to pass the wound immediately, but after passing their rate may be retarded (5-15 seconds per 80 microns). One cell that was punctured seventeen times the same day showed a very prompt return to the normal rate following the last three punctures.



If the change of rate in the streaming protoplasm is a reaction to the wound stimulus it is obvious that this stimulus is not transferred directly any great distance. A wound with a sharp needle, even when very large (200 microns), has never been observed to cause any change of rate in an adjacent node, internode, or leaf cell. If the stimulus is the direct effect of the wound, rather than of the resulting accessory disturbance, such as the loss of protoplasm, the readjustment of the wall, etc., the effect should be manifest before the withdrawal of the needle from the puncture. This is actually the case, since there is a region around the puncture in which all movement ceases momentarily at the time of the puncture and movement may be resumed in portions of this region while the needle is still in the hole formed. With the removal of the needle, and the accompanying outflow of protoplasm, the effect may become general or remain local, as already described. That the disturbance of the protoplasm remote from the wound is due to another factor than the wound stimulus, is indicated by the fact that the non-streaming area does not form immediately, but in the next two or three minutes after the puncture has been made, and its outline is influenced by the direction in which the protoplasm is streaming.

Cannon (2) in the discussion of his experiments on traumatic shock, distinguishes primary shock, which he thinks is probably due to some nervous disturbance, and secondary shock, which he ascribes to some toxic element. This toxic substance, possibly a proteid cleavage product, enters the circulation and causes disturbances in the system that are manifest sometime after the wound has been received. The time between the injury and the development of the secondary shock may be hours, or it may be weeks.

The phenomena in the *Nitella* cell suggest perhaps a similar situation. The cessation or retardation of movement which may immediately result from the puncture may be a matter of direct stimulation. Lillie (13) believes that any local stimulus alters the plasma-membrane, and this starts an electric current which is propagated through the cell membrane and thus the transmission of the stimulus is very rapid. This stimulus thus propagated, produces a response throughout the cell, which he compares to the "none or all" response of a muscular fibre.

Bayliss (1) working on *Amoeba* and *Nitella* was able to show that a weak electric current would change the moving protoplasmic hydro-sol to a non-motile gel. This gel reverts to the sol and movement re-commences as soon as the current is removed.

A primary effect of this sort may or may not be evident in *Nitella*, but what apparently corresponds to the secondary effect always follows the puncturing of a *Nitella* cell. When the needle enters the cell more or less protoplasm is injured. Toxic substances liberated by this injured protoplasm may be responsible for the subsequent changes in the streaming. Retardation or cessation of streaming may be due to the fact that the protoplasm becomes more viscous or passes into a gel. As would be expected, this region is not well developed on the side where the cytoplasm is moving toward the wound and the toxic substance has to diffuse against the stream, or is limited to the area through which it can diffuse during the time of rest. On the other side of the wound the toxic substance may be carried by the current present, which explains the gradual development of the reaction in this region as well as its more permanent character.

A toxic substance, formed by the injured protoplasm and present in the region washed by the cytoplasm passing the wound, might account for the effect on the plastids in this section. If the protoplasm in this region remains quiet for any length of time the plastids die, lose their color, and finally disintegrate. Plastids that are much nearer the wound, but are not in contact with this protoplasm, remain normal.

Such a substance must be assumed to be given off by the wound for some time, two or four hours, since the moving protoplasm is retarded for this length of time, as it passes the wound. This retardation is not the result of a purely mechanical obstruction by the internal plug, for the amount of retardation gradually lessens until it disappears, while the internal plug remains for days.

Fitting (6) found that an extract of filter paper contained a substance which would start active rotation in the quiet protoplasm in the cells of *Vallisneria* and *Elodea*. He obtained more pronounced results when he used an extract made from the leaves of *Vallisneria* or *Elodea*. A leaf of *Vallisneria* mounted

in water, and then cut, lost sufficient juice into the water to stimulate movement in the uninjured cells of the leaf. He believed the movement was caused by some substance from the cells, since the protoplasm failed to show any movement if the leaf was washed with fresh water as soon as the cut was made.

These experiments seem to contradict the results obtained with *Nitella*, in which wound substance, as I have interpreted my experiments, seems to check streaming. The contradiction may however be only apparent. It is not impossible that *Nitella* cells also may liberate a similar substance to that which Fitting postulates, which aids in the recovery of motion in the quiet area.

The increased immunity to the toxic substance manifested after several punctures suggests the possibility that an anti-toxin or an anti-body of some character may have developed in the protoplasm. The gradual recovery of the injured area as it is washed by the normal protoplasm also suggests such a possibility.

Hörmann (11) Ewart (5) and later investigators, Bayliss (1), Pfeffer (15) state that any decrease in the viscosity of the cytoplasm results in an increased velocity of movement. Repeated puncturing with its accompanying loss of protoplasm may cause a large absorption of water and a decrease of viscosity. That a very large amount of water can be introduced into the protoplasm without serious injury has been shown by the experiments of Chambers (3). A lower viscosity of the protoplasm may be a factor influencing the time necessary for the streaming to regain its normal rate.

I wish to thank Professor R. A. Harper for his interest and assistance in this investigation, which was carried on at Columbia University, while on leave from Oberlin College.

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## Notes on Fabaceae—VI

PER AXEL RYDBERG

### XYLOPHACOS: VI. GLAREOSI

This group is characterized by the densely woolly, short, more or less incurved fruit, and the loosely villous pubescence of the leaves. The corolla is purple, or ochroleucous with a purple-tipped keel.

Corolla 2-3 cm. long.

Calyx-teeth nearly half as long as the tube; bracts subulate; pod strongly incurved.

Stems usually 1-3 dm. high; pod 2-2.5 cm. long, bent at the middle; corolla purplish..... 32. *X. inflexus*

Stem less than 1 dm. long; pod about 2 cm. long, abruptly bent above the middle; corolla ochroleucous, the keel tipped with purple..... 33. *X. incurvus*

Calyx-teeth less than one-third as long as the tube; stems usually less than 1 dm. long.

Leaflets obovate, mostly rounded to retuse at the apex.

Calyx black-hairy; corolla bluish, 2.5-3 cm. long. 34. *X. funereus*

Calyx white-hairy; corolla rose-purple, white or ochroleucous.

Pod comparatively sparingly hairy; bracts subulate, slightly longer than the pedicels; corolla 2 cm. long, ochroleucous or white. .... 36. *X. nudisiliquus*

Pod very densely villous; bracts lanceolate, more than twice as long as the pedicels.

Leaves densely white-floccose; corolla about 2.5 cm. long, rose-purple..... 35. *X. utahensis*

Leaves sparingly white-villous; corolla about 2 cm. long, ochroleucous..... 37. *X. subvillosus*

Leaflets elliptic or lanceolate, acute or obtuse.

Corolla ochroleucous or white, the keel only tipped with purple..... 38. *X. Purshii*

Corolla purple or purple-tinged.

Peduncles usually not exceeding the leaves.

Leaflets oblanceolate, acute; pod rather long-acuminate..... 39. *X. glareosus*

Leaflets elliptic, obtuse; pod short-acuminate.

Calyx white-hairy..... 40. *X. candelarius*

Calyx black-hairy..... 41. *X. ventosus*

Peduncles in flower usually exceeding the

leaves; pod short-acuminate..... 42. *X. leucolobus*

Corolla 15 mm. long or less.

Corolla ochroleucous; leaflets broadly obovate. . . . . 43. *X. argentinus*

Corolla purplish; leaflets narrowly obovate or oblanceolate.

Racemes usually more than 6-flowered, on very short peduncles; bracts lanceolate, scarcely exceeding the pedicels. . . . . 44. *X. lectulus*

Racemes 2-6-flowered, shorter than the peduncles; bracts subulate, almost half as long as the calyx. 45. *X. lagopinus*

32. *XYLOPHACOS INFLEXUS* (Dougl.) Rydberg. This species has been confounded with *X. Purshii* on one hand and *X. utahensis* on the other, especially when found in undeveloped specimens. Well developed ones have stems 2-3 dm. long, while in the other two species the stems are always very short. In *X. inflexus*, however, the calyx-lobes are much longer, nearly half as long as the calyx-tube. The bracts and pods are longer, and the latter more curved at the middle.

WASHINGTON: Vasey; Alamota, *Piper* 1492, 2938, in 1896, 1899 and 1901; Elmer 283; Wawawai, *Piper*, in 1901; Elmer 112; Hull; Spokane County, *Sandberg & Leiberg* 18; Walla Walla, *Wilkes Expedition* 529; opposite Alkali, *Howell*, in 1882; Illia, *Piper* 665; Spokane, *Piper* 2288; without locality, *Brandegee* 722; Whitman Co., *Elmer* 283; *Sheldon* 8031; Spokane, *Piper* 2288; Klickitat Co., *Suksdorf* 35, 1881 (determined as *A. Purshii longilobus* Jones).—OREGON: Independence, *Cusick* 1366; Wal-lowa County, *Sheldon* 8031; 8276; Snake River, *Cusick* 2522.—IDAHO: Clear Water, *Spalding*; *Sandberg*, *MacDougal & Heller* 9; Lewiston, *Heller* 3010; *Henderson*; Curlew Gulch, *Mulford*.—MONTANA: Helena, *F. W. Anderson*, *Kelsey*; Lo Lo, *Elrod* 114; St. Ignatius, *MacDougal* 285; Missoula, *MacDougal* 126, 236; Sand Coulee, *Williams* 746; Madison, *Scribner* 27d; Hamilton, *Blankinship* 671; Missoula, *Paulson* 58.

33. *Xylophacos incurvus* Rydberg, sp. nov. Subacaulescent perennial, with a cespitose caudex; stems 1-5 cm. long, densely leafy; leaves 5-9 cm. long; stipules lanceolate, 4-5 mm. long, villous-canescens; leaflets 11-17, oblanceolate or elliptic, acute at each end, 10-15 mm. long, 2-4 mm. wide, villous-canescens; peduncles 3-5 cm. long; racemes 3-7-flowered, dense; bracts subulate, 5-10 mm. long, attenuate; calyx white-villous, the tube about 1 cm. long, 3.5 mm. broad, the teeth subulate, 5-7 mm. long; corolla nearly 2 cm. long, white or tinged with rose-purple, the keel purple-tipped; banner obovate, retuse; wings

about 2 mm. shorter, the blade oblong, acutish, shorter than the claw; keel-petals still shorter and broader, the blade strongly arcuate and rounded at the apex; pod densely white-villous, 2 cm. long, 1 cm. broad and 7 mm. deep, usually sulcate on both sutures except at the apex, strongly incurved almost to a half circle; seeds obliquely reniform, brown, 2.5 mm. long, 2 mm. broad.

Type collected in California, in 1875, *Lemmon* 76 (herb. Columbia University).

This might have been included in *A. Purshii longilobus* M. E. Jones, (*Zoe* 4: 269. 1893), but the type of the latter was from Tehachapi, Southern California. In his Revision of *Astragalus*, Jones modifies his description and evidently includes several diverse forms.

CALIFORNIA: *Lemmon* 75; Modoc County, *M. S. Baker*, in 1893; Plumas County, *Heller & Kennedy* 8727; Sierra County, *Lemmon* 51; Upper Sacramento, *Parkinson*.—NEVADA: Carson City, *C. L. Anderson*, in 1864.

34. *Xylophacos funereus* (Jones) Rydberg. (*Astragalus funereus* M. E. Jones, *Contr. W. Bot.* 12: 11. 1908). Jones compares this species with *X. coccineus*. To me it seems more related to *X. utahensis*, differing in the larger flowers and fruit and in the black-hairy calyx. It does not have the narrow and almost straight petals of *X. coccineus* and the pod is more curved as in *X. utahensis*. I have seen specimens only from the type locality, Rhyolite, Nevada, but Jones gives also the Charleston Mountains and at Tonopah, Nevada, and Darwin, California.

35. *XYLOPHACOS UTAHENSIS* (Torr.) Rydberg. This was first described as *Phaca mollissima utahensis* from specimens collected by Stransbury on the northeast shore of Great Salt Lake and on Stansbury Island, though it had been collected before by Fremont in 1845. It is distinguished by the broadly obovate leaflets densely white-villous with matted hairs, the short calyx-teeth and bracts, the peduncles usually exceeding or equaling the leaves, the rose-purple corollas, in drying turning bluish.

UTAH: Numerous collections.—MONTANA: Beaverhead County, *Shear* 3350; *Payson & Payson* 1909; *Tweedy* 12.—WYOMING: Uinta County, *A. Nelson* 2065.—IDAHO: Shoup, *Kemp* 70; Challis, *Macbride & Payson* 3224; 1764.—NEVADA: Washoe County, *Kennedy* 997; *Sretch*, in 1865.



36. *Xylophacos nudisiliquus* (A. Nels.) Rydberg. (*Astragalus nudisiliquus* A. Nels. Bot. Gaz. 54: 410. 1912.) Nelson described this from fruiting specimens and his description is therefore inadequate. Jones, probably not having seen the type, claimed that it is only an aged form of *A. glareosus*. The habit of the plant, however, is not like that of *X. glareosus* but that of *X. utahensis*. The main difference being in the pod, which in the present species is sparingly hairy and strongly incurved above the middle. There are two specimens from Malheur County, Oregon, which I take to be the same, *Leiberg 2003* in flower and *Leiberg 2243* in late flower and young fruit. Both these are less densely hairy than the type, *Nelson & Macbride 1088*. The fruit of *Leiberg 2243* is similar to that of the type, but younger and hence more thin-walled, the corollas of *No. 2003* are evidently ochroleucous and about 2 cm. long, the calyx white-villous, its tube about 1 cm. long and its teeth subulate and 2-3 mm. long; the bracts are narrower than in *X. utahensis* and much shorter than in *X. inflexus*.

37. *Xylophacos subvillosus* Rydberg, sp. nov. Cespitose perennial with a much branched caudex; stems 5 cm. long or less, leafy; leaves 5-6 cm. long; stipules narrowly lanceolate, 5 mm. long; leaflets 9-15, obovate or oval, 5-12 mm. long, 3-5 mm. wide, rather sparingly white-villous, rounded at the apex; peduncles 2-6 cm. long; racemes 2-6-flowered; bracts linear-attenuate, 4-5 mm. long; calyx loosely villous, the tube 8-9 mm. long, 3 mm. wide, the teeth subulate, 2-3 mm. long; corolla apparently ochroleucous, about 18 mm. long; banner rather broadly obovate, retuse; wings shorter, the blade acutish, oblong; pod densely villous, scarcely 2 mm. long, nearly 1 cm. broad, evenly arcuate throughout.

Type collected in Sierra Valley, California, in 1873; *Lemmon* (herb. N. Y. Bot. Gard.).

The type was labelled by Lemmon *Astragalus eriocarpus* and the duplicate in the Gray herbarium was determined as *A. glareosus*. It has no very close relationship to either, but comes nearest to *A. utahensis* from which it differs in the sparser pubescence and smaller ochroleucous flowers.

CALIFORNIA: Sierra Valley, *Lemmon*, in 1873; without locality, *Kellogg & Hartford 193*.—OREGON: Harney County, *Peck 2797* (This is referred here doubtfully).

38. *XYLOPHACOS PURSHII* (Dougl.) Rydberg. The plant

was independently described as *Astragalus Purshii* Dougl. from flowering specimens, and *Phaca mollissima* Nutt. from fruiting ones. *A. lanocarpus* Sheld. is nothing but a small-flowered typical *X. Purshii*. Jones, in his Revision, admits 5 varieties of *Astragalus Purshii*. Of these three represent as many good species. The var. *longilobus* I have been unable to place, and var. *interior* is, as far as I know it, of no consequence. It is rather superfluous to cite specimens of this species. Its range extends from British Columbia to Saskatchewan, South Dakota, Nebraska, and Nevada. Specimens cited from California do not belong to it. Specimens in fruit distributed as *A. Booneanus* belong here.

39. XYLOPHACOS GLAREOSUS (Dougl.) Rydberg. This species has been much misunderstood and confused with both *X. Purshii* and *X. inflexus*. Jones for a long time applied the name *A. glareosus* to *X. argophyllus*, and Sheldon redescribed it as *A. allanaris*, perhaps led astray by Jones' application of the name. A. Nelson again redescribed it as *A. Booneanus*, though some of the fruiting specimens referred to the latter belong to *X. Purshii*. *X. glareosus* much resembles in habit *X. argophyllus* and the most important difference is in the fruit. Jones in his Revision made it a variety of *Astragalus inflexus*, but it would have been more proper to make it a variety of *X. Purshii*, and it is more closely related to that species than are *X. leucolobus* and *X. lectulus* which Jones regards as varieties of *A. Purshii*.

The characters separating it from *X. Purshii* are, the purple corolla, the usually longer peduncles and the pod, which is less densely hairy and abruptly incurved above the middle.

BRITISH COLUMBIA: Lake Osoyoos, *Macoun* 70443.—WASHINGTON: Spokane County, *Sandberg & Leiberg* 18; Chelan County, *Griffith & Cotton* 168; Ellensburg, *Piper* 2680; Yakima County, *Cotton* 552 in part; 1107; *Henderson* 2356; Klickitat County, *Suksdorf* 50; *Whited* 1275 and 18; Ellensburg, *Whited* 273.—OREGON: Malheur County, *Leiberg* 2202, 2158; Morrow County, *Leiberg* 32; Wasco County, *Lawrence* 128, 369; Baker County, *Peck* 10385; Eastern Oregon, *Cusick* 1367, 2522; Lake Co., *Eggleston* 6894, 7023; 6842.—IDAHO: *Burke*; Elmore County, *Macbride & Payson* 2850; Canyon County, *Macbride* 57, 760, 785; Weiser, *Jones* 6228; also *June Clark* 5, 22; *Mulford*, in 1892.—UTAH: Cache County, *C. P. Smith* 2365.—WYOMING:

Uintah County, *Merrill & Wilcox* 583; *A. Nelson* 2999, 2990; *Parry* 79; Newcastle, *Bates*.—MONTANA: Beaverhead County, *Nelson & Nelson* 5416; Belgrade, *Blankinship* 674.

40. *Xylophacos candelarius* (Sheldon) Rydberg. (*Astragalus candelarius* Sheldon, Minn. Bot. Stud. 1: 143. 1894.) This is related to *X. Purshii*, differing mostly in the smaller purplish flowers and more densely pubescent and obtuse leaflets. It is evidently the same as *Astragalus Purshii tinctus* M. E. Jones (*Zoe* 4: 269. 1893), at least as to the type, though the specimens cited from Ventura and Inyo Counties, California, do not belong to it. It also includes *Astragalus consectus* Sheldon in part. Jones erroneously refers this species to his *Astragalus Newberryi Watsonianus*, i. e. *Xylophacos Watsonianus* (Kuntze) Rydb.

NEVADA: Esmeralda County, *Shockley* 33; Carson City and Virginia City, *Bloomer*; Wasco County, *Sonne* 1, 11; Mt. Gabb, *Purpus* 5867; Pioche, *Minthorn* 31 (?)—CALIFORNIA: Nevada County, *Sonne*, in 1887 and 1895; Siskiyou County, *Greene* 713; *Brown* 470; *Baker* 3557; Modock County, *Austin & Bruce* 2207; *G. D. Butler* 1283; *Manning* 715; Palmetto Range, *Purpus* 5879.—OREGON: Mitchell, Wheeler County, *Peck* 10112.

41. *Xylophacos ventosus* (Suksdorf) Rydberg. (*Astragalus ventosus* Suksdorf Ms.) Perennial, with a tufted cespitose caudex; stems many, less than 5 cm. long, white-villous, densely leafy; leaves spreading, 2–5 cm. long; stipules lanceolate acuminate, 5–6 mm. long. Leaflets elliptic, obtuse, 5–7 mm. long, 2–3 mm. wide, white-villous on both sides, peduncles 1–2 cm. long; racemes 3–6-flowered, sub-capitate; bracts lance-subulate, 5 mm. long; calyx black-villous, often purple-tinged, the tube 10–11 mm. long, 2–3 mm. broad, the teeth subulate, 2 mm. long; corolla purplish, about 2 cm. long; banner obovate; wings slightly shorter, the blades oblong, with a large basal auricle; keel-petals slightly shorter, the blade, strongly lunate, rounded at the apex; pod ovate, lunate, fully 1.6 cm. long, 8 mm. broad and deep, densely woolly.

Type locality; Windy rocky places several kilos east of Bingen, Nov. 10, 1920, *Suksdorf* 10662.

The species is related to *X. candelarius* and *X. glareosus*, but differs from both in the black-hairy calyx, from the former in the somewhat larger pod and from the latter in the broader obtuse leaflets.

WASHINGTON: Klickitat County, *Suksdorf* 10662, 50, and 5916; Rattlesnake Hill, Yakima Co., *Cotton* 552.

42. *Xylophacos leucolobus* (S. Wats.) Rydberg. (*Astragalus leucolobus* S. Wats.; M. E. Jones, *Zoe* 4: 270. 1893.) This resembles closely the preceding, but the peduncles usually exceed the leaves, the calyx is often purple-tinged and densely short-villous, its lobes are very short, the pod is more tapering and the wing-petals almost equalling the banner.

CALIFORNIA: San Bernadino County, *Parish* 2349, 2998, 4966, 3744, 1813; Inyo County, *Coville & Funston* 543, 783, 496; *Elmer* 3995; *Abrams & MacGregor* 236; Ventura County, *Munz* 7014a; *Grinnell*.

In specimens from the Tehachapi Mountains of Kern County, the calyx is more long-hairy, its teeth longer, and the bracts subulate attenuate and scarious. *Astragalus consectus* Sheldon was evidently a mixture of three or four species, but the type, not seen by me, apparently belongs to this form.

CALIFORNIA: Kern County, *Abrams & MacGregor* 432; *Eastwood* 3230; *Dudley* 314; *Pringle*, in 1882; *Jones*, in 1897; *Heller* 7712.

43. *Xylophacos argentinus* Rydberg, sp. nov. Subacaulescent caespitose perennial; stems very short and leafy; leaves 4-7 cm. long; stipules lanceolate, 5 mm. long; leaflets 7-13, broadly obovate, about 1 cm. long, rounded or truncate at the apex, silvery-villous; peduncles 3-5 cm. long; bracts lance-subulate, 3-4 mm. long; racemes 2-5-flowered; calyx white-villous, the tube 5-6 mm. long, the teeth subulate, 2-3 mm. long; corolla ochroleucous, 13-14 mm. long; banner obovate; wings slightly shorter, the blades linear, acutish; keel-petals broader, arcuate and rounded at the apex; pod densely white-villous, about 2 cm. long, 8 mm. deep, arcuate above the middle, the sutures slightly sulcate.

Type collected at Lone Pine, California, May 14, 1897, *Jones* (Gray Herbarium).

It resembles *X. utahensis* in leaf-form, pubescence and the fruit, but the corolla is much smaller and ochroleucous.

CALIFORNIA: Inyo County, *Jones* (type); *Heller* 8313.

44. *Xylophacos lectulus* (S. Wats.) Rydberg. (*Astragalus lectulus* S. Wats. Proc. Am. Acad. 22: 471. 1887.) This resembles *X. candelarius* a good deal, but is smaller, more tufted, with very short peduncles, smaller pod and much smaller flowers, less than 15 mm. long. The pubescence is more like that of *X. utahensis* but the leaflets are narrower. *Jones* regards it as a variety of *A. Purshii*.

CALIFORNIA: San Bernadino Mountains, *Parish* 1812, 2348, 2997; *Parry & Lemmon* 95; Sonora Pass, *Brewer* 1908, 1882.

45. *Xylophacos lagopinus* Rydberg, sp. nov. Cespitose perennial with a branched caudex; stems 2-10 cm. long, canescent; leaves ascending, 3-5 cm. long; stipules lanceolate, about 5 mm. long; leaflets 5-9, mostly 7, obovate, 5-10 mm. long, rounded at the apex, silvery-villous; peduncles 1-4 cm. long; racemes 2-6-flowered; bracts lance-subulate, 3-4 mm. long; calyx villous, the tube 4-5 mm. long, 2-2.5 mm. wide, the teeth 1-1.5 mm. long; corolla purplish, about 12 mm. long; banner obovate; wings shorter, the blades lance-linear, acutish; keel-petals much shorter, strongly arcuate and rounded at the apex; pod densely villous, 1.5 cm. long, 1 cm. deep, slightly inflexed.

Type collected on plains between Preneville and Bear Buttes, Crook County, Oregon June 25, 1894, *Leiberg* 326 (herb. N. Y. Bot. Gard.).

Jones (*Astragalus* 224. 1923), included this in *Astragalus Purshii lectulus*, but it differs in the better developed stems and peduncles, longer bracts, fewer flowers, and fewer leaflets.

OREGON: Crook County, *Leiberg* 326; *Cusick* 1951a, 2824; *Whited* 3029a; *E. Nelson* 825; Wheeler County, *Peck* 10112, 9745; Summer Lake, *Bailey* 70; Pumice Plains, *Leiberg* 4297; Lake Co., *Eggleston* 6838, 6877; Laidlaw, *Whited* 51.

## VII. COCCINEI

This group is easily distinguished from the rest of the species by its large crimson flowers fully 3 cm. long. It contains only one species.

46. *XYLOPHACOS COCCINEUS* (Parry) Heller.

CALIFORNIA: San Diego County, *Orcutt*; *Spencer* 235; *Mearns* 3026; *Brandege*, in 1891; *Eggleston* 19818; Inyo County, *Heller* 8190; *Austin*; *Matthews*; *Coville & Funston* 491; San Bernadino County, *Parish* 1280; Darwin, *Jones*, in 1897; San Jacinto, *Leiberg* 3176.

## Studies on the flora of northern South America—VII\*

H. A. GLEASON

### NEW OR NOTEWORTHY SPECIES OF MELASTOMATACEAE—II

#### *Saccolena* n. gen.

Flowers 5-merous; calyx 10-winged, turbinate, elongated in fruit; petals yellow, obovate; stamens dimorphic; filaments flattened; anthers oblong, opening by a terminal pore, the connective prolonged at base above the insertion of the filament, the conspicuous posterior appendage subulate in the short stamens, ovoid and saccate in the long stamens; ovary superior, 3-winged, turbinate, broadly truncate at the apex.

Cogniaux, in his monograph of the Melastomataceae, recognized seven genera in the tribe Bertolonieae, distinguished fundamentally by the location of the staminal appendage. In the four essentially Andean genera *Diplarpea*, *Monolena*, *Diolena*, and *Triolena*, the appendage is anterior, while in the three Brazilian or Amazonian genera *Bertolonia*, *Macrocentrum*, and *Salpinga*, it is either posterior or else virtually none. *Saccolena* closely resembles *Salpinga* in its trumpet-shaped fruiting calyx, and its relationship is further shown after dissection by the posterior appendage. The two genera differ chiefly in the structure of the stamens and the appendage. In *Salpinga* they are isomorphic, with a slender or subulate erect appendage and also with a short basal posterior spur, while in *Saccolena*, they are dimorphic, not only in length, but also in the character of the appendage, while the short basal spur is lacking. The genus is known only by its type species, which is here described.

*Saccolena dimorpha* n. sp. Stems herbaceous, branching from the base, simple above, 10-20 cm. tall, 4-angled, minutely pulverulent with reddish resinous globules, the internodes about 1 cm. long; petioles very slender, minutely pulverulent, 12-25 mm. long; leaf-blades broadly ovate, dark green, thin and membranous, the principal ones 30-55 mm. long by 20-32 mm. wide, narrowed or barely acuminate to an obtuse tip, sparsely and minutely ciliate-denticulate, broadly rounded below to an inequilateral base, glabrous, 3-5-nerved, the veinlets inconspicuous; racemes axillary, 6-8-flowered, the peduncles strongly wing-

\* Contributions from the New York Botanical Garden, No. 276.

angled, 1-2 cm. long, rhachis 10-15 mm. long; pedicels slender, strongly wing-angled, gradually expanded into the obconic, glabrous, 10-winged hypanthium, together 11 mm. long; calyx-limb 0.8 mm. long; sepals somewhat spreading, triangular, 3.8 mm. long, 2.3 mm. wide, sharply acute, glabrous, faintly veined, with a narrow central wing; petals apparently broadly ovate, yellow, at least 11 mm. long, very thin and membranous; filaments thin and transparent, flat, 1-nerved, 0.7 mm. wide, 2.8 mm. or 4.3 mm. long; anthers oblong, truncate, opening by a terminal pore, 1.5 mm. long, 0.7 mm. wide, the connective 0.8 long above the insertion of the filament, appendage of the short stamens geniculate near the base, subulate, 2.7 mm. long by 0.3 mm. in diameter, appendage of the long stamens ovoid, saccate, 2.3 mm. long, 1.1 mm. wide; fruiting calyx and the strongly thickened pedicel 2 cm. long, prominently wing-angled, expanded at the throat. FIG. 1.

Type, *Bro. Ariste-Joseph A 920*, collected at Paimé, Dept. Cundinamarca, Colombia, and deposited in the herbarium of the New York Botanical Garden.

*Diolena lanceolata* n. sp. Stems herbaceous, branched at the base, simple above, 6-10 cm. tall, closely and densely appressed-pilose above, glabrate below, the internodes about 5 mm. long; leaves firm, narrowly oblong-lanceolate, the largest 35 mm. long by 6 mm. wide, long-acuminate to an obtuse apex, flat or somewhat revolute, barely undulate to entire, sparsely and minutely pilose-ciliate, narrowed at the base into a pilose petiole 1-2 mm. long, bluish-green and glabrous above, closely strigose along the basal portion of the midvein, very sparsely pilose on the surface, especially toward the apex, 3-nerved, the obscure veinlets 2-3 mm. apart, ascending; racemes 2-flowered, from the upper axils, the peduncle pilose like the stem, 3-5 mm. long; pedicels pilose, 2 mm. long; flowers 5-merous; hypanthium broadly campanulate, 3 mm. long and wide, densely strigose, terete above, obtusely 3-winged on the basal 2 mm.; calyx-limb membranous, 0.4 mm. wide, the sepals broadly triangular, 0.6 mm. long, 1 mm. wide, barely apiculate, the exterior teeth subulate-conic, glabrous, 0.6-0.7 mm. long, the free portion of the sepal reduced to a mere line across the inner face of the exterior tooth; petals white, ovate-oblong, obtuse, glabrous; anthers broadly oblong with parallel sides, minutely 4-lobed at the apex, barely tapering at the base, the connective barely prolonged basally, terminated posteriorly by 2 minute, ovoid, saccate lobes 0.05 mm. long, anteriorly by 2 erect, filiform, straight or slightly curved appendages somewhat surpassing the anther; filaments flattened; style stout, terete, glabrous, the stigma capitate; capsule obconic, 3 mm. long, 5-6 mm. wide, 3-winged, glabrate at maturity. FIG. 2.

Type, *Killip 11,537*, collected at Santa Rosa, Dept. El Valle, Colombia, alt. 200-300 m., 22 Sept. 1922, and deposited in the herbarium of the New York Botanical Garden. The sheet exhibits several ripe capsules, but only one unopened flower, from which the above description was made. Its petals are 2.5 mm. long, the anther 1 mm., the anterior appendages 1.2 mm., the filament 0.7 mm., the style 2.6 mm. These dimensions may be too small for the mature flower. The leaves of each opposite pair are somewhat unequal, the smaller averaging two-thirds the length of the larger. *Diolena lanceolata* is obviously related to *D. pileoides* Triana and *D. agrimonioides* Triana. Both the latter have a much denser indument; in the former the smaller leaves are greatly reduced in size, and in the latter the leaves are conspicuously dentate.

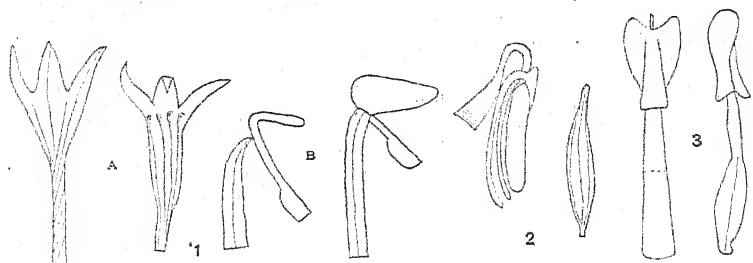


FIG. 1. *SACCOLENA DIMORPHA* Gleason: A, hypanthium and twisted pedicel  $\times 2$ , fruiting hypanthium natural size; B, stamens  $\times 10$ . FIG. 2. *DIOLENA LANCEOLATA* Gleason, leaf natural size, stamen  $\times 15$ . FIG. 3. *MICONIA KILLIPII* Gleason, dorsal and lateral face of stamens  $\times 10$ .

*LEANDRA RUFESCENS* (DC.) Cogn. This variable species might easily be divided into several, if attention were paid to characters as minute as those used in various other genera, such as the character, amount, and distribution of pubescence and the details of the venation. Among the recognizable forms, *La Cruz 4480*, from Kaieteur Falls, British Guiana, seems worthy of note. Here the leaves are almost entire, the denticulation being indicated merely by longer cilia at fairly regular intervals. Transverse veinlets between the margin and the outermost vein are absent. Pubescence is completely absent on the upper surface of the leaf, even on the primary veins, at maturity, and rarely extends within the outermost veins even on the young leaves. The calyx is more sparsely hirsute, with less



conspicuous furfuraceous pubescence beneath the hairs, and the ovary is less strongly pubescent at the summit.

*Leandra purpurea* n. sp. Stem shrubby, 15 dm. high obtusely 4-angled above, later becoming terete, softly hirsute with both glandular and simple spreading hairs 1-1.5 mm. long; petioles stout, channeled above, 2-4 cm. long, hirsute like the stem, but more densely; leaf-blades thin and membranous, ovate-elliptic, sharply and obliquely acuminate, sharply and saliently denticulate (2-5 teeth per cm. of margin, setose, 0.5-1 mm. high) and sparsely ciliate, rounded at the base, upper surface dark green, persistently sparsely pubescent with curved-ascending hairs 0.5 mm. long, densely hirsute on the nerves with erect hairs 1.5-2 mm. long, lower surface paler, softly and thinly pubescent and very sparsely glandular, 5-nerved, the veinlets obscure above, elevated beneath; panicles terminal, 12-15 cm. long, the axes and branches densely hirsute with purple-red simple and glandular hairs, branches divaricate, verticillate; flowers 5-merous, mostly sessile, or the terminal on pedicels 3-8 mm. long, bractless; hypanthium nearly spherical, cinereous, densely pubescent with simple hairs about 0.5 mm. long and sparsely glandular-hirsute with hairs 1 mm. long; berries blue, sparsely villous and glandular, 8 mm. in diameter, spherical; seeds oblong, 0.45 mm. long, with a triangular lateral appendage at the end.

Type, *Gleason 89*, collected in dense upland forest at Tumatumari, British Guiana, 18 June-8 July 1921, and deposited in the herbarium of the New York Botanical Garden. The leaves of each pair are somewhat unequal, the largest one measuring 19 cm. long by 10.5 cm. wide and its opposite 17 cm. by 9 cm. The petiole of the larger leaf is regularly twice as long as that of the smaller. The pubescence of the stem is brown in color as far as the base of the first panicle-branch, above which it is conspicuously red-purple as far as the hypanthium. The proportion of glandular hairs increases steadily to the apex of the inflorescence. *L. purpurea* is obviously related to numbers 189-193 of Cogniaux's monograph and shows various points of resemblance to *L. verticillata* (L. C. Rich.) Cogn., *L. inaequalifolia* (Schr. & Mart.) Cogn., and *L. polyadena* Ule. It differs from *L. verticillata* in its longer petioles, broader leaves persistently pubescent above, quadrangular branches, and glandular pubescence; from *L. inaequalifolia* in its longer petioles, its erect, purple-red panicle with verticillate branches, and in the greater uniformity in size of the leaves of each pair, and from *L. polyadena*

in its non-glandular, softly pubescent leaves with 5 green nerves, its softer pubescence on the stem, and its shorter sepals.

Among our recent collections of melastomes are three sheets of *Miconia rostrata* (Naud.) Cogn., Pittier 5886, Pittier 10,441 and E. Pittier 152, from Venezuela, and two sheets of *Miconia Benthamiana* Triana, Killip 7791 and 11,454, from Colombia. Both species have been collected repeatedly in the past, and the present specimens add nothing to our knowledge of their distribution. They have anthers tapering to the apex and octomerous flowers, and were accordingly included by Cogniaux in the section *Octomeris*. But in all superficial characters and habit they suggest at once the genus *Heterotrichum*, and in fact are so closely similar to *H. macrodon*, *H. octonum*, and *H. glandulosum*, even in their more recondite characters, as to raise some doubt as to the validity of generic lines as at present drawn in this region of the family. Throughout the tribe Miconieae the anthers show a considerable degree of uniformity, principally in the absence of the distinctive structural features which are so characteristic of most other tribes, and the genera have been separated largely on the position of the inflorescence, the character of the fruit, and the shape of the petals. In his key to the genera of this tribe, Cogniaux distinguished the two genera only by the nature of the exterior calyx-teeth: "nulli vel inconspicui" in *Miconia*, and "saepius subulati quam interiores majores" in *Heterotrichum*. *Miconia* is also stated to have a 2-5-locular ovary, in contrast to the 6-12-locular ovary of *Heterotrichum*. Our two species actually have 8-locular ovaries, as is beautifully shown on Bentham's plate 34 in the Botany of the Sulphur Expedition for *M. Benthamiana*. The anthers and filaments are essentially the same for *Heterotrichum* and for *Miconia* section *Octomeris*. The only remaining distinction seems to be in the mere length of the external calyx-teeth, a purely quantitative character certainly without generic value. In fact, Naudin combined the two groups in the genus *Octomeris*, a union which seems entirely justifiable and logical, although the differentiation of a special genus for these octomerous plants is hardly necessary. Because of the general similarity in habit and structure to the well-known *Heterotrichum octonum* (Bonpl.) DC., our two species would better be united with it generically, and the following transfers are accordingly proposed.

**Heterotrichum rostratum** (Naud.) new comb.

*Octomeris rostrata* Naud. Ann. Sci. Nat. Bot. III. 4: 53. 1845.

*Miconia rostrata* Cogn. Monog. Phaner. 7: 752. 1891.

**Heterotrichum polyandrum** (Benth.) new comb.

*Clidemia polyandra* Benth. Bot. Sulph. 95. pl. 34. 1844.

*Miconia Benthamiana* Triana, Trans. Linn. Soc. 28: 102. 1871.

The petals are pale purple, 10 mm. long, rather than 4 mm., as stated by Cogniaux (cf. Bentham's plate); the stamens were 40 in each of two flowers examined, and 24 in one flower of Killip 11,454. This sheet also has broadly round-ovate leaves almost glabrous above, and shorter, less dense pubescence on the stem.

**Amphitoma** n. gen.

Flowers 5-merous; hypanthium campanulate; sepals short, the exterior teeth subulate, much exceeding the sepals; petals broadly elliptic, obtuse; stamens 10, all alike; anthers oblong to obovate, 2-celled, introrse, opening by two broad, confluent, terminal pores, the connective prominently thickened below and minutely saccate at the base posteriorly; filaments short, somewhat flattened, the lower portion stout or turgid, the upper slender; ovary mostly inferior, 3-locular, the summit rounded; style straight, terete, subclavate; stigma truncate; fruit baccate, the calyx persistent; seeds smooth, obovoid. Woody plants with strongly flattened, two-edged stems (whence the generic name), opposite leaves with flattened petioles, and terminal, rounded, corymbiform panicles of pedicelled, orange-yellow flowers.

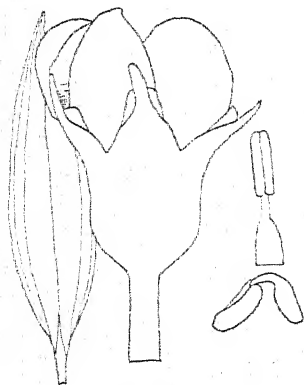


FIG. 4. Flower and stamens  
X 5, leaf natural size.

**Amphitoma flavescens**, n. sp.

Fruticose; young stems sparsely stellate-puberulent, soon glabrescent, strongly and persistently flattened, sharply 2-winged; leaf-blades thick and firm, oblong-lanceolate, 7-11 cm. long, 12-30 mm. wide, long-acuminate and somewhat falcate, minutely spinulose-denticulate, cuneate at base into a strongly flattened, distally dilated petiole about 1 cm. long, upper surface slightly bullate, minutely punctate, but essentially glabrous, lower surface yellowish green, thinly stellate-tomentulose, especially on the veins, 5-nerved, the outer pair arising from

the intermediate pair about 5 mm. above the base, veinlets 1-1.5 mm. apart, lightly impressed above, prominently elevated and reticulate beneath; panicles terminal, soon appearing lateral by the growth of branches from the uppermost axils, the rhachis and branches flattened below, angulate above, thinly stellate-puberulent, the ultimate branches 3-5 mm. long, jointed at the middle; hypanthium pale brown, 3.5 mm. long and wide, sparsely stellate-puberulent; calyx prolonged 0.7 mm. above the staminal torus; sepals ovate-triangular, 1.3 mm. long, broadly rounded, the free margin scarious; exterior teeth subulate, erect, 2 mm. long, exceeding the sepals by 1 mm.; petals glabrous, 4.5 mm. long, 4 mm. wide, somewhat inrolled; filaments 2 mm. long, glabrous, the lower two-thirds stout, ovoid, 0.8 mm. wide at base, the upper third slender; anthers 1.7 mm. long; ovary glabrous at the summit, radially 10-ribbed; style glabrous, 3-4 mm. long, gradually thickened upwards to 0.6 mm. in diameter; stigma truncate. FIG. 4.

Type, *Killip 11,884*, collected in forest at "La Gallera," Micay Valley, Dept. El Cauca, Colombia, alt. 1800-1900 m., 29, 30 June 1922, and deposited in the herbarium of the New York Botanical Garden. A second sheet, *Killip 7930*, was collected at the same place and altitude 1 July 1922, while the Kew herbarium contains two specimens by Lehmann, numbered 7637 and 8247. In *Killip 7930*, the panicles are fruiting and considerably enlarged, measuring 10 cm. long from the lowest branch; the leaves are as much as 14 by 3.5 cm., more strongly bullate above, and, as a corollary, more heavily reticulate beneath.

It is a matter for regret that a new genus should be described in the tribe Miconieae, where generic lines are already rather weakly drawn. But I have not been able to assign this remarkable plant to any established genus without a considerable extension of the generic boundary. According to Cogniaux's key, it stands near *Heterotrichum*, agreeing with that particularly in its long exterior calyx-teeth, but having a 3-locular ovary, shorter stamens, and an entirely different habit. Its stamens are distinctly those of a *Miconia*, although they vary in shape even in the same flower, from the oblong ones of *Eumiconia* to the obovate ones of *Cremanium*, but the elongate exterior calyx-teeth are quite unlike *Miconia*.

*Miconia polita* n. sp. Section Jucunda; fruticose, 2 m. high, strictly glabrous to the inflorescence; stems brown, terete or nearly so, the upper internodes flattened, elongate; petioles

slender, 3-3.5 cm. long; leaf-blades pale green, shining, rigid but thin, lance-elliptic, 22-24 cm. long, 7-8 cm. wide, acuminate to a blunt tip, entire, remotely spinulose-ciliate, narrowed to an acute base, 5-nerved, the veinlets conspicuous, 6-9 mm. apart; peduncle terminal, glabrous, 3 cm. long; panicle pyramidal, 9 cm. long, branches spreading, 2-4 at each node, sparsely glandular-villous, especially at the nodes; pedicels 2-3 mm. long, glandular-villous; flowers 5-merous; hypanthium cylindric, 5 mm. long, 2 mm. wide, obscurely 10-nerved, sparsely glandular-villous with spreading hairs 0.6 mm. long; sepals spreading, triangular-acuminate, 1.3 mm. long, 1.5 mm. wide at the base, acute, sparsely glandular-villous like the hypanthium; petals white, narrowly obovate-oblong, 5 mm. long, 2.3 mm. wide, obtuse, glabrous, membranous, finely nerved; filaments filiform, glabrous, 3 or 5 mm. long; anthers subulate, strongly introrse-arcuate, 3.5 mm. long, opening by an oblique introrse pore, the anther-sacs prolonged 0.2-0.3 mm. and rounded at base; connective not prolonged, unappendaged, glabrous; ovary mostly free, glabrous, 3-locular, the summit broadly rounded and retuse; style straight, declined, 10 mm. long, glabrous; stigma punctiform.

Type, *Gleason 53*, collected in dense upland forest, Tumatumari, British Guiana, 18 June-8 July 1921, and deposited in the herbarium of the New York Botanical Garden. The remarkably shining surface of the leaves is unique in the section. Mr. N. E. Brown has noted on the type sheet "This is identical with an unnamed *Miconia* in the British Museum labelled 'Guiana Belgica, Alex. Anderson.' "

*MICONIA GUIANENSIS* (Aubl.) Cogn. This is probably the commonest melastomataceous tree in British Guiana. It certainly is the most abundantly represented in herbaria, possibly because of its conspicuous clusters of white-bracted flowers. Our ample series of specimens shows a considerable range of variation, among which three deserve special mention. Here the leaves are distinctly obovate and rounded above to a short cuspidate tip. They are *La Cruz 2373* and *2805*, from the upper Mazaruni River, and *La Cruz 1716*, from the upper Rupununi River.

*MICONIA MACROTIS* (Griseb.) Cogn. The section *Adenodesma* is characterized by glandular connectives at the base of the anthers. This species, characterized by huge leaves deeply auriculate-cordate at base, is represented in our collections by a recent

specimen from Trinidad, *E. G. Britton 2840*, as well as by older material by Kuntze and Broadway. It should be noted that the glandular nature of the connective is very obscure, and I have not been able to observe it until after boiling and carefully isolating a stamen under a considerable magnification. On such treatment it is also seen that the base of the anther-sacs is considerably prolonged, a character foreign to most *Miconias*. The anthers are 5-5.5 mm. long, and abruptly narrowed above the middle into a very slender apex. The petals are narrowly obovate and densely stellate-tomentose externally.

The flowers are undoubtedly 6-merous, with a 4-locular ovary, although Cogniaux states that 5-merous flowers characterize the section. Cogniaux, in his monograph, doubtfully refers here also a specimen from Ecuador, collected by Poortmann, which I have not seen, but which may well be the same as *Hitchcock 21,315*. The latter agrees precisely with the Trinidad sheets in foliage and hypanthium, the stem is more closely velutinous, the petals have the same shape, and the anther-sacs are similarly prolonged. But certain differences are as striking as these similarities, and have led me to distinguish it as a variety.

*Miconia macrotis canescens* n. var. Petals canescent externally with short, straight, simple hairs; anthers 8 mm. long, gradually tapering from base to apex.

Type, *Hitchcock 21,315*, collected between Porto Velo and El Tambo, Prov. Oro, Ecuador, alt. 600-1000 m., 2 Sept. 1923, and deposited in the herbarium of the New York Botanical Garden.

There is not only great habital similarity between *M. macrotis*, of the section *Adenodesma*, and *M. Boisseriana* Cogn., a Cuban species of the section *Tamonea*, but also a strong resemblance in other more recondite points of structure. Both seem to be derivatives of the widely distributed *M. macrophylla* (D. Don) Triana.

*Miconia plumosa* n. sp. • Small tree, 5 m. tall; stems stout, densely hispid-tomentose with recurved-spreading, slightly plumose, brown hairs 3-4 mm. long and straight, more or less reflexed, densely plumose hairs 2 mm. long; petioles hispid like the stem, 5 mm. long; leaves of each pair strongly unequal, the blades thick and firm, obovate-oblong, entire, abruptly narrowed at the apex to a subulate-triangular cusp 1 cm. long, gradually tapering below to a truncate or rounded base 10-15

mm. wide, upper surface dull green and glabrous, lower surface thinly stellate-pubescent and strongly reticulate, 3-ply-nerved, the midvein closely stellate-tomentose for half or more of its length and also sparsely pilose with spreading simple hairs 2-3 mm. long, the lateral veins arising 3-7 cm. above the base, glabrous, the veinlets conspicuous, 5-8 mm. apart; panicle cylindrical, narrow, crowded, 2 dm. long, hispid like the stem, the lateral branches 2-5 mm. long, bearing 2-7 sessile, 5-merous flowers; bractlets linear-subulate, 5-8 mm. long; hypanthium urceolate-campanulate, 5 mm. long, densely stellate-tomentose; sepals broadly triangular, obtuse, 1 mm. long; ovary 3-locular, depressed at the summit; seeds obovoid-prismatic, truncate, 1 mm. long.

Type, *Gleason 901*, collected on dry sandhills, east of Rockstone, British Guiana, 22-30 July 1921, and deposited in the herbarium of the New York Botanical Garden. It is a member of the section *Adenodesma* and related to *M. tomentosa* (L. C. Rich.) D. Don, from which it differs in its strongly hispid stem, its hispid midvein, its rounded leaf-bases, and its more congested panicle. The type specimen bears only the two uppermost leaves, measuring 22 by 9 and 41 by 20 cm.

*Miconia imbricata* n. sp. Arborescent; branches terete or nearly so, densely and coarsely furfuraceous-tomentose with dark brown hairs; petioles stout, 6-10 mm. long, pubescent like the stem; leaf-blades narrowly oblong-obovate, thick and firm, 5-7 cm. long, 2-3 cm. wide, obtuse or abruptly subacuminate to an obtuse apex, narrowed from above the middle to an obtuse base, minutely spinulose-ciliate, 5-nerved, upper surface dull yellowish-green, glabrous, somewhat rugose, with prominently impressed veins and veinlets, lower surface dull brown, pubescent, especially on the veins, with crooked or crisped, black or brown hairs; panicles terminal, 3-5 cm. long, lax, few-flowered, pubescent like the stem; flowers 5-merous, on pedicels 4-8 mm. long; hypanthium campanulate, 5 mm. long, 4 mm. in diameter at the summit, minutely and scabrously pubescent, with a few long hairs at the top; calyx prolonged 1 mm. beyond the hypanthium, somewhat flaring; sepals round-ovate, 1.9 mm. long, 2.8 mm. wide, obtuse, the free margin glabrous, membranous, white, exterior teeth stoutly subulate, erect, sparsely short-hirsute, equaling the sepals; petals white, broadly rotund, 9 mm. wide, 7 mm. long, strongly retuse, glabrous, many-nerved, widely overlapping; anthers (not fully mature) lanceolate, 3.8 mm. long, 1.2 mm. wide at base, tapering to the obtuse apex, the connective slightly thickened on the back toward the base and minutely 2-saccate; filaments about 4 mm.

long, strongly flattened, glabrous; ovary 5-locular, the summit conspicuously truncate-conic, 5-ribbed, glabrous; style 4 mm. long, straight, terete, glabrous; stigma truncate, not expanded, 0.6 mm. in diameter.

Type, *Pennell 10,503*, collected in mossy forest, Cerro Tatama, Dept. Caldas, Colombia, alt. 3200-3400 m., 8-10 Sept. 1922, and deposited in the herbarium of the New York Botanical Garden. It is a member of the section *Octomeris*, related to species 62-65 of Cogniaux's monograph, but differing from them in many features of size, shape, and pubescence.

***Miconia rupicola* n. sp.** Stems shrubby, obscurely 4-angled, minutely and sparsely stellate-furfuraceous above, glabrescent with age, sparsely setose in the axils; petioles slender, 8-18 mm. long, stellate-furfuraceous above, glabrate beneath; leaf-blades firm, obovate-oblong, 8.5-10.5 cm. long, 4-5.5 cm. wide, broadly obtuse or rounded above to a minute, ovate, blunt apex, minutely and remotely denticulate, obtuse at base, glabrous and densely punctate above, thinly furfuraceous beneath, especially on the veins, 5-nerved, the outer pair obscure, veinlets inconspicuous and reticulate; panicle 5 cm. long, lax, few-flowered, stellate-furfuraceous; flowers 8-merous, sessile or on pedicels 1-3 mm. long; bud broadly fusiform, blunt, 8 mm. long, rupturing irregularly below the middle; hypanthium broadly campanulate, minutely stellate; petals 8 mm. long, glabrous externally.

Type, *Killip 11,685*, collected on exposed cliffs, Buenaventura, Dept. El Valle, Colombia, alt. 0-10 m., 5-10 Oct. 1922, and deposited in the herbarium of the New York Botanical Garden. It differs from *M. notabilis* Naud., the only other 8-merous species of the section *Laceraria*, in its furfuraceous pubescence, its broader and blunter leaves, its shorter pedicels, and its glabrous petals.

***Miconia Smithii* Cogniaux, n. sp.** Arborescent, 6-10 m. high; stems obscurely 4-angled and minutely stellate-furfuraceous when young, terete and glabrescent with age; petioles slender, 20-25 mm. long, thinly stellate-pubescent; leaf-blades subcoriaceous, narrowly ovate-oblong, 8-11 cm. long, 3.5-4.5 cm. wide, abruptly short-acuminate to an obtuse apex, entire or obscurely and remotely undulate, rounded at base, shining and glabrous above, or minutely puberulent along the lower portion of the midvein, minutely stellate-pulverulent beneath, 5-nerved; panicle 8-10 cm. long, stellate-pubescent, its branches spreading, simple, spiciform; flowers 5-merous, sessile, approximate above, becoming 3-6 mm. apart; hypanthium broadly campanulate, 2 mm. long, glabrous; sepals subscarious, semi-



circular, 0.5 mm. long, 1 mm. wide, glabrous, minutely erose on the margin; petals broadly ovate, obtuse, 2 mm. long, entire, glabrous; filaments 2.3 mm. long, glabrous, the lower two-thirds flat, 0.5 mm. wide, the upper one-third slender; anthers linear, 1.7 mm. long, glabrous, the connective thickened below and bearing an ascending posterior appendage 0.2 mm. long; ovary rounded at the summit, glabrous; style straight, 3 mm. long, glabrous, gradually thickened upward to a truncate stigma.

Type, *Smith 1846*, collected in open mountain forest, Sierra del Libano, alt. 6000 ft., Santa Marta, Columbia, 27 Feb. 1899, and deposited in the herbarium of the New York Botanical Garden. It is a member of the section *Eumiconia*, subsection *Diplostachyae*, and stands according to the arrangement in Cogniaux's monograph, next to *M. Mendoncae* Cogn., a Brazilian species with large, thin, sharply acuminate, serrulate, ciliate leaves and furfuraceous calyx.

*Miconia panicularis* n. sp. Stems woody, prominently flattened and densely brown-velutinous with stellate hairs above, becoming terete and glabrate in age; petioles stout, flattened above, 10-15 mm. long, densely velutinous; leaf-blades dark green, membranous, oblong-obovate, 25 cm. long by 12 cm. wide at maturity, abruptly and sharply acuminate, entire, narrowed from the middle to the acute base, essentially glabrous above, minutely and very sparsely stellate-pulverulent beneath on the surface, more densely so along the veins, 5-nerved, the outer pair less prominent but extending to the apex, veinlets conspicuous, 7-9 mm. apart; panicle broadly pyramidal, 15 cm. long and wide, the rhachis densely stellate-velutinous, the branches thinly so; pedicels 0.5 mm. long, thinly stellate-furfuraceous; flowers 5-merous; hypanthium campanulate-cylindric, 1.6 mm. long, minutely and sparsely stellate, especially at the base; sepals broadly depressed-triangular, 0.6 mm. long, puberulent, membranous and rounded at the apex, the exterior teeth conic, 0.2 mm. long; petals apparently white, narrowly obovate, 2.3 mm. long, 1.1 mm. wide, narrowed to the base, rounded at the apex, glabrous; filaments filiform, glabrous, 2.7 mm. long; anthers linear-oblong, 2.3 mm. long, obtuse at the apex, truncate and minutely bigibbous at base posteriorly, opening by a single terminal pore, the connective not prolonged; summit of ovary hemispheric, glabrous, with 10 rounded ribs; style stout, straight, terete, glabrous, 3.7 mm. long, 0.4 mm. in diameter; stigma truncate, 0.6 mm. in diameter; fruit globose, 3 mm. in diameter, nearly glabrous, the calyx-limb persistent.

Type, *La Cruz 4445*, collected at Kaieteur Falls, Potaro River, British Guiana, 23 Oct.-3 Nov. 1923, and deposited in

the herbarium of the New York Botanical Garden. Other collections are *La Cruz* 4434, from the type locality, *La Cruz* 3908 and 3957, from the Wanama River, and *La Cruz* 3737, from the Waini River, Northwest District, British Guiana. The description of the fruit is taken from the last specimen. The species is a member of the section *Eumiconia*, and related to *M. Beurlingii* Triana, from which it differs in its broader and larger leaves, more abruptly acuminate, and with more prominent tertiary veins, less densely stellate hypanthium, longer sepals, and more densely pubescent inflorescence. One of the specimens was noted by the collector as a tree 20 ft. high.

***Miconia caucana* n. sp.** Stem irregularly flexuous, freely branched, probably scandent, thinly stellate-tomentulose when young, glabrescent with age; petioles slender, 5–10 mm. long, tomentulose like the stem; leaf-blades membranous, oblong-elliptic, varying to oblong-obovate or narrowly ovate, 5–7 cm. long, 18–25 mm. wide, sharply acuminate, entire, acute or cuneate at base, upper surface dark green, sparsely pilose with subappressed straight hairs about 0.6 mm. long, lower surface pale green, stellate-tomentulose on the veins, minutely stellate-pulverulent on the veinlets, 3-nerved; panicles numerous, terminating all the branches, 2–4 cm. long, lax, few-flowered, the rhachis and branches stellate-tomentulose; flowers 5-merous, on pedicels 1–2 mm. long; hypanthium campanulate-cylindric, faintly 10-ribbed, 2.2 mm. long, thinly stellate; sepals triangular, 1 mm. long and wide, sharply acuminate, conspicuously reflexed, minutely pubescent, the exterior teeth conic-subulate, equaling the sepals; petals apparently yellow, oblong-obovate, 3.5 mm. long; anthers linear, 3.2 mm. long, opening by a single terminal pore, the connective dilated at base anteriorly into two ovoid, introrse appendages 0.2 mm. long; filaments filiform, glabrous, 3.3 mm. long; ovary summit hemispheric, glabrous, minutely 10-ribbed; style slender, somewhat declined, 6.3 mm. long, slightly thickened near the apex to the truncate stigma.

Type, *Holton* 909, collected at La Paila, Dept. El Cauca, Colombia, 18 Apr. 1853, and deposited in the herbarium of Columbia University at the New York Botanical Garden. It is a member of the section *Eumiconia*, subsection *Paniculares*, although its foliage resembles that of *M. ambigua* (Bonpl.) DC. and *M. virescens* (Vahl) Triana, of the subsection *Seriatiflorae*. Under the arrangement of Cogniaux's monograph, it may be placed near *M. gracilis* Triana and *M. hyperprasina* Naud.

*Miconia pulvinata* n. sp. Frutescent, 1.5 m. high; stems obscurely 4-angled, setose at the nodes, otherwise glabrous; leaf-blades deep green, membranous, oblong, 19-25 cm. long, 6.5-9.5 cm. wide, acute or subacuminate, prominently crenate-serrate and ciliate, acute or cuneate at base, glabrous above, sparsely hirtellous beneath, especially on the veins, 5-nerved, the outer pair obscure, the intermediate pair near the margin, the veinlets conspicuous beneath, strongly ascending; petioles stout, 5-7 mm. long, glabrous beneath, densely pilose above; panicle slender, pilose-tomentose at the nodes, the smaller branches more or less pubescent; bracts minute, narrowly triangular, hirtellous; flowers 5-merous, sessile, secund; hypanthium glabrous; calyx truncate, the sepals reduced to minute teeth, persistent on the globose, blue fruit.

Type, *Smith 1841*, collected in the mountain forest at Las Patidas, Santa Marta, Colombia, 25 Jan. 1899, and deposited in the herbarium of the New York Botanical Garden. The character of the inflorescence, the setose nodes, the 5-nerved leaves, and the truncate calyx leave no room for doubt as to its close relationship to *M. racemosa* (Aubl.) DC., which is an Amazonian species extending west into Venezuela. Our species differs conspicuously in its narrower leaves on very short, densely pilose petioles.

*Miconia virgulata* n. sp. Stems slender, woody, obtusely 4-angled, the upper internodes alternately glabrous and densely tomentose on the four sides, the tomentum deciduous on the lower internodes, which remain distinctly verrucose; petioles slender, 4-7 mm. long, glabrous below, densely pilose-tomentose near the apex, especially on the upper side; leaf-blades firm, narrowly lanceolate, 45-75 mm. long, 7-13 mm. wide, subacuminate, prominently pilose-ciliate, acute at base, dark green above, brownish-green beneath, glabrous on both sides, 3-nerved; panicles 3-4 cm. long, the rachis pubescent like the stem, the lateral branches short, spreading, nearly glabrous; bractlets minute, ovate, fimbriate-ciliate; flowers sessile, secund, 5-merous; hypanthium campanulate, 2 mm. long, glabrous; sepals minute, broadly rounded, 0.3 mm. long, glabrous; petals oblong-obovate, 1.5 mm. long, truncate, glabrous; anthers thick, oblong, 1.2 mm. long, opening by a single terminal pore, the connective not prolonged at base; filaments slender, 1.4 mm. long.

Type, *Jenman 7441*, collected on the Curiebrong (Kuribrong) River, British Guiana, Oct. 1898, and deposited in the herbarium of the New York Botanical Garden. Although distributed as a Jenman collection, the name of the actual collector is not known.

*M. virgulata* is another relative of *M. ciliata* and *M. racemosa*, as shown by its secund inflorescence, its nearly truncate calyx, its pubescent petioles, and its strongly ciliate leaves. It is beautifully characterized by the two strips of tomentum on the stem, extending up from the base of each leaf, and is also distinct in general habit, because of its small, narrow leaves and short internodes 5-10 mm. long.

*Miconia Killipii* n. sp. Low tree, 3.6 m. tall; stems obtusely 4-angled, shallowly 4-sulcate, and thinly furfuraceous-pulverulent above, becoming subterete and glabrate with age, thickened at the nodes; petioles slender above a conic base, 13-17 mm. long, pulverulent like the stem; leaf-blades thin but firm, ovate-oblong, 8-11.5 cm. long, 4-5.5 cm. wide, short-acuminate to a broad, obtuse tip, entire, broadly rounded below to a truncate base, glabrous, 5-plexi-nerved, the outer pair obscure, the intermediate pair arising 2-3 mm. from the base; veins lightly impressed above, prominently elevated beneath, veinlets about 6 mm. apart, obscure above, prominulous beneath; panicle 13 cm. long, sparsely branched, widely spreading, furfuraceous-pulverulent like the stem, the rhachis 4-sulcate, the smaller branches nearly or quite terete; bracts none or caducous; pedicels 2-3 mm. long; flowers 5-merous; hypanthium broadly campanulate, 2.5 mm. long, 3.5 mm. wide, thinly pulverulent; sepals thick and heavy, broadly triangular, 0.9 mm. long, nearly 2 mm. wide, obtuse, exterior teeth none; petals pink-blue, short-ovate from a broadly truncate base, 3.3 mm. long, 4 mm. wide, glabrous within, minutely pulverulent without; anthers thick, broadly ovate, 2.4 mm. long, 1.3 mm. wide, rounded at the apex, the anther-sacs 1.7 mm. long, opening by a single minute terminal pore, connective thickened on the back and strongly thickened below the anther-sacs; filaments stout, flattened, 2-2.3 mm. long, 1.2 mm. wide at base, the distal half (and the base of the connective) densely glandular; ovary truncate at the summit; style 4 mm. long, thickened upward from 0.6 mm. in diameter at the base to 1.0 mm. at the summit; stigma peltate, flat, 2.1 mm. in diameter. FIG. 3 (see page 375).

Type, *Killip II, 415*, collected along open trail at La Cumbre, Dept. El Valle, Colombia, alt. 1600-1800 m., II, 19, Sept. 1922, and deposited in the herbarium of the New York Botanical Garden. The plant is a member of the section *Amblyarrhena*, and of the general affinity of *M. grandiflora* Cogn., *M. majalis* Cogn., and *M. floribunda* (Bonpl.) DC. It differs from these in the size of the flower, the size, shape, and pubescence of the foliage, and above all in its remarkable ovate anthers. I have

not been able to compare it with two other species of the group, *M. macrantha* Triana and *M. lamprarrhena* Triana, neither of which was seen by Cogniaux. Of these, the former is described with much larger flowers, and the latter agrees with our plant in only a single point of description, the puberulent petals.

*Miconia scutata* n. sp. Stems woody, essentially terete and glabrous below the inflorescence; petioles stout, glabrous, 6-10 mm. long, expanded at base into a spreading, corky or cartilaginous, horseshoe-shaped appendage 1-2 mm. wide; leaf-blades oblong, thick and firm, 15-23 cm. long, 5.5-7 cm. wide, obtuse or subacute at the apex, minutely and remotely denticulate, cuneate to the base, dull green and glabrous above, very minutely and sparsely rufescent-punctate beneath, especially along the veins, 5-nerved, the outer pair obscure and submarginal; panicles widely spreading, freely branched, the rhachis and branches sharply angled, minutely furfuraceous-punctate; pedicels less than 1 mm. long; flowers 5-merous; hypanthium subcylindric, 2.5 mm. long, obscurely punctulate; sepals membranous, oblong-obovate, 0.6-0.8 mm. long, truncate or obtuse, the exterior teeth flat, appressed, triangular, 0.5 mm. long; petals obovate from a narrow base, 2.3 mm. long, broadly rounded at the apex; anthers oblong, blunt, thick, 2.3 mm. long, 0.8 mm. wide, opening by a terminal pore 0.3 mm. wide, slightly attenuate at base, the anther sacs minutely prolonged anteriorly and the connective posteriorly (about 0.1 mm.); filaments slender, slightly flattened, 3.3 mm. long, glabrous, attenuate in the upper third; ovary-summit conic, glabrous, with 10 radial ribs prolonged around the style into erect, linear appendages 0.3-0.4 mm. long; style slender, 6 mm. long, glabrous, minutely thickened upward; stigma capitate, 0.8 mm. in diameter.

Type, *Hitchcock 21,868*, collected in the valley of the Pastaza River, between Banos and Cashurco, 8 hours east of Banos, Prov. Tungurahua, Ecuador, alt. 1300-1800 m., 25 Sept. 1923, and deposited in the herbarium of the New York Botanical Garden. It is related to *M. stipularis* Naud. and *M. annulata* Triana, of the section *Amblyarrhena*, and is distinguished from them by the dilated petiole, the shape of the leaf, and the prolonged ridges on the ovary.

## Chamber with thermostatic control and rotating table for plant cultures

SAM F. TRELEASE

In attempting to work out plans which will allow certain problems of the salt relations of plants to be attacked in their simplest form, attention has been directed to the initial behavior of germinating seeds.<sup>1</sup> Satisfactory duplication of the experimental conditions in successive series of tests appears less difficult to secure in experiments with very young seedlings than in those with plants in later phases of growth. The whole question of photic environment may be avoided, since such tests can be carried on in darkness, and the temperature conditions to which the plants are subjected may be more easily controlled. Although consistent results have been obtained in repetitions of these experiments without artificial control of temperature, nevertheless it has seemed desirable to employ controlled temperatures in order to have greater certainty in the effective duplication of the influential experimental conditions as well as to test the effects of temperature differences. A study has therefore been made of means of controlling temperature, and this paper describes the culture chamber at present in use. The chamber automatically maintains any desired temperature between 10° and 35° C., with a range of variation not exceeding  $\pm 0.5^\circ$  C. It is of simple construction, resembling an ordinary refrigerator, and is equipped with a rotating table and a thermostat composed of standard commercial appliances that are easily assembled. Although essentially the same devices are probably in use in many laboratories, descriptions of them are not readily available in the literature. A description of the apparatus may therefore be of interest to workers having similar needs, in physiology, pathology, or bacteriology.

The lower diagram of figure 1 is a longitudinal section of the chamber. The outside dimensions are 57 inches wide, 34 inches deep (to go through an ordinary door), and 40 inches high. The walls are insulated with 7/8-inch spruce, two layers

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<sup>1</sup> Trelease, Sam F., and Helen M. Trelease. Growth of wheat roots in salt solutions containing essential ions. *Bot. Gaz.* 80: 74-83. *f. 1, 2.* 1925.

of water-proof paper, 2 inches of sheet cork, two layers of water-proof paper, and 7/8-inch oak, the last on the outside. The chamber has 6-inch metal legs, and is raised from the floor by a wooden stand 24 inches high.

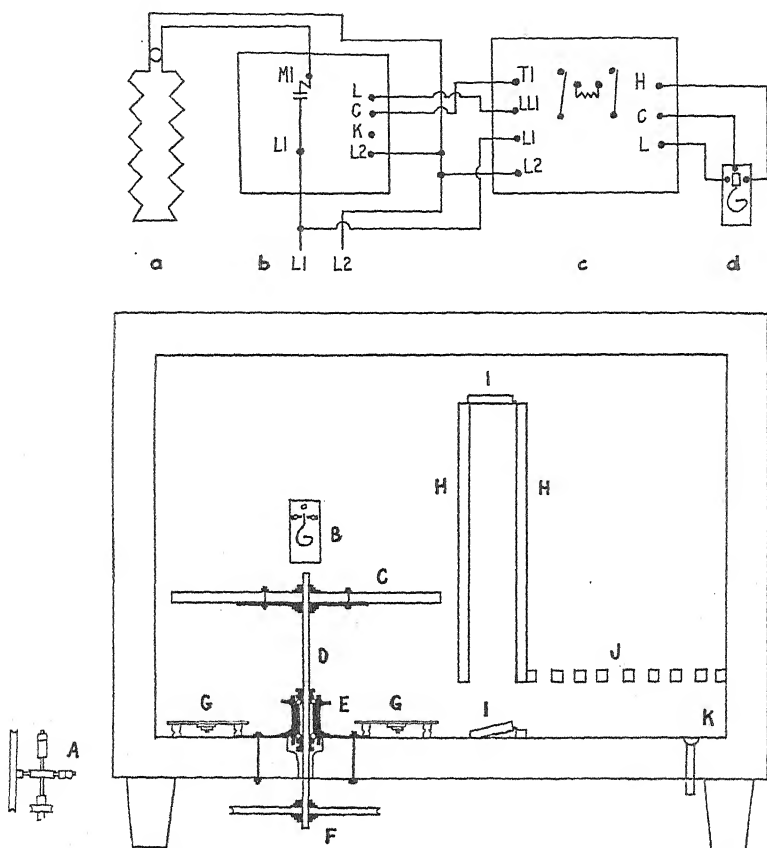


FIG. 1. Culture chamber for maintaining any desired temperature between  $10^{\circ}$  and  $35^{\circ}$  C.

Upper diagram: Wiring connections for heating units (a), magnetic switch (b), magnetic relay (c), and thermo-regulator (d).

Lower diagram: Longitudinal section of chamber, showing reducing gear (A), thermo-regulator (B), rotating table (C), shaft (D), motor-cycle hub (E), pulley (F), heating units (G), baffle boards (H), dampers (I), ice rack (J), and drain (K).

The culture compartment (at the left) is  $24\frac{1}{4}$  inches wide,  $26\frac{1}{2}$  inches deep, and  $32\frac{1}{2}$  inches high; and the ice compart-

ment (at the right) is  $17\frac{1}{4}$  inches wide,  $26\frac{1}{2}$  inches deep, and  $32\frac{1}{2}$  inches high. The compartments are separated by two 1-inch baffle boards (H) of spruce, 4 inches apart, extending to within 4 inches of the top and to within 5 inches of the bottom of the chamber. A 1-inch partition separates the floor of the ice compartment from that of the rest of the chamber. Dampers (I) that may be operated from the outside of the box serve to regulate the size of the openings above and below the right-hand baffle board, and thus control roughly the circulation of cool air from the ice chamber. A galvanized-iron rack (J) supports ice, when needed, and a drain (K) is provided in the floor.

The culture compartment has a door (24 inches wide and 30 inches high) fitted with three glass plates separated by air layers, permitting inspection of the cultures. A removable curtain of black cloth hangs in front of the door on the outside. Access to the ice compartment is had through another door (15 inches wide and 23 inches high). The entire interior of the ice compartment, the baffle boards, the dampers, and the floor of the culture compartment are covered with galvanized iron. Heavily insulated electric wires lead through two  $\frac{1}{4}$ -inch metal tubes in the floor.

In many kinds of biological experimentation it is essential that all comparable cultures be exposed to practically the same temperature conditions, even though fluctuations in temperature are permissible. Such uniformity of exposure is readily obtained by means of the rotating table introduced by Livingston<sup>2</sup> and Shive.<sup>3</sup> It is a pleasure to express indebtedness to Dr. B. E. Livingston, of the Johns Hopkins University, for valuable suggestions regarding the construction of the rotating table here used. The circular table (C) shown in the diagram is 23 inches in diameter and composed of two layers of  $\frac{7}{8}$ -inch white pine with grain crossed to hinder warping. A circular steel plate ( $\frac{3}{16}$  inch thick and 12 inches in diameter) is fastened by four bolts to the bottom of the table. To facilitate air circulation, the marginal part of the table, for a distance of  $5\frac{1}{2}$  inches in from the

<sup>2</sup> Livingston, B. E. A rotating table for standardizing porous cup atmometers. *Plant World* 15: 157-162. f. 1, 2. 1912.

<sup>3</sup> Shive, J. W. A study of physiological balance in nutrient media. *Physiol. Res.* 1: 327-397. f. 1-14. 1915.



edge, is perforated by many  $\frac{1}{2}$ -inch holes. Also, six rectangular pieces of sheet "tin," attached to the bottom of the table, tend to stir the air gently and direct currents upward as the table rotates. The table contains a hole at the center and is supported on a threaded steel shaft (D) by means of flanged lock-nuts ( $2\frac{1}{4}$  inches in diameter) with washers (4 inches in diameter). The upper part of the shaft (D) is a solid steel rod ( $\frac{5}{8}$  inch in diameter) slightly tapered and driven into the hollow cylindrical axle-bushing of a Harley-Davidson motor cycle front wheel; the middle part of the shaft is the axle-bushing itself, which is threaded and bears cones turning on ball bearings; and the lower part of the shaft is a solid rod driven into the lower end of the axle-bushing. The front-wheel hub (E) is fastened to a circular steel plate (similar to that bolted to the table) by machine screws passing through the spoke holes. The steel plate, with a heavy rubber gasket, is held in place by four bolts. The lower end of the shaft passes through the floor of the box and bears a wooden pulley (F), 14 inches in diameter, held in place by lock-nuts with washers. The pulley is connected by a  $\frac{1}{4}$ -inch round belt to a "plant rotator" reducing gear (A), supplied by the Eberbach and Son Company of Ann Arbor, Michigan. The gear is turned by a  $\frac{1}{4}$ -horse-power motor (making 1160 rotations a minute). When geared in this way, the table makes a rotation once in 40 seconds. Motor and gear are supported on a stand by themselves, so that their vibrations are not transmitted to the rest of the apparatus.

The temperature near the level of the rotating table is automatically maintained by heat supplied by electric heating units (G) controlled by a thermo-regulator (B) that actuates a relay and switch (located outside the chamber) which open and close the electric circuit through the heating units. A wiring diagram of the thermostat is shown in the upper part of figure 1. The lines supply direct current, 110 volts. A bimetallic thermo-regulator (d) controls heating units (a) through a magnetic relay (c) and a magnetic switch (b).<sup>4</sup> The arrangement is such that when the temperature falls below that for which the thermo-

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<sup>4</sup> The thermo-regulator and relay (kindly suggested to the writer by Dr. G. L. Peltier, of the University of Nebraska) are supplied by the Johnson Service Co., of Milwaukee, Wis.; and the magnetic switch is made by the Cutler-Hammer Mfg. Co., of Milwaukee, and designated as no. 193.

regulator is set, the tongue makes contact at the left and closes the circuit through the thermo-regulator and the electro-magnet of the relay; the relay responds so as to close the circuit through the electro-magnet of the switch, which in turn closes the circuit through the heating units. As the temperature rises, the tongue of the thermo-regulator moves away from the contact at the left; and when contact is made at the right, the relay opens the circuit through the electro-magnet of the switch, and a powerful spring breaks the circuit through the heaters. Although the heaters actually carry only about 2 amperes, this thermostat is rated as capable of controlling a current of 50 amperes.

The heating units are similar to those described by Peltier and Goss.<sup>5</sup> Two are connected in series, a pilot light indicating when current is flowing through them. Each has 19 feet of no. 24 nichrome wire<sup>6</sup> wound on a strip of transite (hard asbestos-board) 1 inch wide, 17½ inches long, and ¼ inch thick. This strip is bolted to the lower side of a rectangular piece of transite (7 inches wide and 17½ inches long, and perforated by many ⅜-inch holes drilled about ¾ inch apart), the strip being separated ¼ inch from the larger piece by means of a small square of transite placed at each end. An iron bolt with two nuts holds the three pieces of transite together at each end of the heating unit and also serves as a binding post for wiring connections. The heating unit stands on four porcelain insulators bolted to the transite. The two heating units, connected in series, carry about 1.82 amperes and use 200 watts (on 110 volts), their resistance being 60.4 ohms. The heating power can, of course, be increased by shortening the heating coils, or decreased by lengthening the coils or using a rheostat outside the chamber.<sup>7</sup> As Clark<sup>8</sup> points out, for very accurate temperature control, the heating power of the coils should be adjusted so that the time during which the regulator leaves the heat on, is about as long as the time during which the regulator leaves the

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<sup>5</sup> Peltier, G. L., and R. W. Goss. Control equipment for the study of the relation of environment to disease. Coll. Agric. Univ. Nebraska Agric. Exp. Sta. Bull. 28: 1-16. 1924.

<sup>6</sup> Nichrome wire is made by the Driver-Harris Co., of Harrison, N. J.

<sup>7</sup> The heat supplied is proportional to the wattage (amperes × volts, or volts<sup>2</sup> ÷ ohms, or amperes<sup>2</sup> × ohms).

<sup>8</sup> Clark, W. M. The determination of hydrogen ions. 2nd ed.; Baltimore. 1922.

heat off; or so that the heating rate is about equal to the cooling rate. This insures a regular oscillation about the mean temperature.

The thermostat is easily set for any temperature between  $10^{\circ}$  C. and  $35^{\circ}$  C. For a low temperature (below the maximum temperature of the surrounding air), ice is kept in the right-hand compartment and the dampers are adjusted to regulate the circulation of cool air. A temperature considerably lower than  $10^{\circ}$  probably may be obtained by the use of a freezing mixture of ice and salt, conveniently contained in a galvanized iron tank. For a high temperature, no ice, of course, is needed. After initial adjustment of the thermostat, which may require about one hour, the apparatus operates continuously with little attention, aside from the addition of ice when a low temperature is employed.

Without the use of a fan for rapidly stirring the air, it is of course impossible to secure a uniform distribution of temperature throughout the chamber. Nevertheless, the range of fluctuations in temperature near the level of the rotating table does not exceed  $\pm 0.5^{\circ}$  C., and by rotating the cultures near the edge of the circular table all of the cultures are subjected to nearly the same fluctuations. Greater accuracy of control may, of course, be secured by using a more sensitive thermostat, and a more even distribution of temperature throughout the chamber may be obtained by stirring the air by means of a motor-driven fan.

In conclusion, mention should be made of a fact which has doubtless been recognized by many workers, but which is not specially emphasized in the biological literature: namely, that a chamber which gives very accurate results for one portion of the temperature range may give inaccurate results for another portion of the range, although the temperature variation is the same in both cases. This may be illustrated by means of data from Livingston's<sup>9</sup> smoothed growth-temperature graph based upon Lehenbauer's<sup>10</sup> careful studies of maize. If one

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<sup>9</sup> Livingston, B. E. Physiological temperature indices for the study of plant growth in relation to climatic conditions. *Physiol. Res.* 1: 399-420. f. 1-4. 1916.

<sup>10</sup> Lehenbauer, P. A. Growth of maize seedlings in relation to temperature. *Physiol. Res.* 1: 247-288. f. 1-4. 1914.

culture were exposed to a mean temperature of  $31^{\circ}$  C. and if another culture in the same chamber were exposed to a mean temperature of  $32^{\circ}$  C., the corresponding difference in growth rate would amount to only 0.3 per cent—a negligible error in most studies. But if one culture were exposed to  $14^{\circ}$  C. and another to  $15^{\circ}$  C., the difference in growth rate would amount to 20.3 per cent—an enormous error. From cases of this sort it is obvious that the error permissible in temperature control depends not only upon the process studied but also upon the sensitiveness of the process at various portions of the temperature range.

Certain studies on physiological balance in culture solutions, now practically completed with the use of the above described apparatus, are to be reported in a future paper.



# INDEX TO AMERICAN BOTANICAL LITERATURE

1924-1925

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BULLETIN  
OF THE  
TORREY BOTANICAL CLUB

NOVEMBER 1925

A revision of the species of *Radula* of the United States  
and Canada\*

HEMPSTEAD CASTLE

(WITH ELEVEN FIGURES)

RADULA Dumortier, Comm. Bot. 112. 1822

*Martinellius* S. F. Gray, Nat. Arr. Brit. Pl. 1: 690. 1821.<sup>1</sup>

*Stephanina* O. Kuntze, Rev. Gen. Pl. 839. 1891.

Plants green, frequently tinged with brown or yellow: in northern species stems one to several centimeters in length, in tropical species up to one foot in length, prostrate or pendulous and frequently forming depressed mats on rocks, bark, and in a few species on living leaves, more or less loosely and irregularly pinnately and bipinnately branched, in a few species sometimes dichotomous by subfloral innovations, the branches infrafoliar in origin: leaves alternate, more or less imbricate, conduplicate-bilobed; the lobes almost always entire, the ventral lobe smaller, often inflated near the keel, the free margin usually appressed to the dorsal lobe: underleaves entirely wanting: rhizoids usually present and always arising from the mammilliform swelling of the ventral lobe: leaf cells usually uniformly thin-walled, occasionally with marked trigones: species mostly dioicous, a few monoicous: the male inflorescence, in dioicous species, often amentiform, terminal on the stem or a main branch but often proliferating, more rarely intercalary; in monoicous species similar or situated directly below the female inflorescence; male bracts densely imbricate, in two to thirty-five pairs, subequally lobed, much inflated at the base; antheridia single, more rarely in two's or three's: female inflorescence

\* Contribution from the Osborn Botanical Laboratory.

<sup>1</sup> Reasons for using the generic name *Radula* instead of *Martinellius* are presented by M. A. Howe (Mem. Torrey Club 7: 157. 1899) and by A. W. Evans (Trans. Conn. Acad. 8: 265. 1892).

[The BULLETIN for October (52: 355-408) was issued 20 November 1925.]

borne usually on the stem or a main branch, and in most species subtended by one or two subfloral innovations; female bracts a single pair, usually somewhat smaller than the stem leaves; the ventral lobe proportionately smaller and always without rhizoids; archegonia several: perianth in most cases strongly compressed dorsiventrally toward the free end, usually terete toward the base, usually not at all carinate or plicate, the mouth broad, more or less bilabiate, the truncate lips entire, or repand-crenate: calyptra narrowly obovoid or elongate pyriform, rather firm and subopaque, the walls composed of two to three layers of cells: capsule oval-cylindrical, two to four times as long as broad, four-valved to the base, the valves bistratose; radial walls of the outer layer of cells with moniliform or nodular thickenings, radial walls of the inner layer less heavily and more uniformly thickened, delicate transverse striae present on the inner tangential walls in some species: seta stout, usually not much exceeding the perianth at maturity: spores globose, minutely granulate-papillate or subechinate: elaters long and slender, obtuse, and usually bispiral: vegetative propagation by means of discoid gemmae or caducous leaves.

#### KEY TO SPECIES

- a. Plants of tropical, temperate or northern distribution, growing on bark or rocks; monoicous or dioicous; discoid gemmae, when present, small.
  - b. Plants not producing gemmae; with or without rhizoids.
  - c. Leaves exhibiting no tendency to shed the dorsal lobe; plants dioicous.
  - d. Dorsal lobe strongly falcate; pronounced trigones usually present in the leaf cells; plants usually tinged with brown.
  - d. Dorsal lobe not at all or only very slightly falcate; trigones absent or minute; plants usually not tinged with brown.
  - e. Leaves ascending; dorsal lobe spoon-shaped; male inflorescence a long, slender ament; rhizoids present, gemmae absent.
  - e. Leaves wide spreading; plants of plumose habit; rhizoids entirely lacking.
  - c. Leaves exhibiting a marked tendency to shed the dorsal lobe.
  - d. Leaves strongly falcate; dioicous.
  - e. Base of lobule fused to the stem almost its entire length by a straight line; dorsal lobe not extending beyond the stem; male inflorescence intercalary or, if apparently terminal, with a slight proliferation at the tip.
1. *R. tenax*  
2. *R. Bolanderi*  
3. *R. polyclada*  
4. *R. Sullivantii*

- e. Base of lobule free one-third to one-half its length, the free portion auriculate and arching over on the stem; dorsal lobe extending across the stem and usually beyond; male inflorescence amentiform, terminal on the stem or a branch but proliferating slightly at the tip; more rarely intercalary.
  - d. Leaves only slightly falcate; heteroicous.  
Base of lobule free half its length, the free portion not auriculate; dorsal lobe extending across the stem but not beyond.
  - b. Plants producing gemmae; rhizoids present.
  - c. Lobule blunt pointed often with slightly prolonged blunt tip, free basal portion slightly auriculate, extending half-way across the stem—rarely more.
  - d. Perianth not split on one side; female flowers terminal with one or two subfloral innovations.
  - e. Plants paroicous; sexual structures almost invariably present even when gemmae are abundant.
  - e. Plants dioicous; sexual structures rare; especially when gemmae are abundant.
  - d. Perianth split on one side half its length; female flowers usually pseudolateral by the extension of a single innovation; gemmae rare.
  - c. Lobule usually broadly rounded at the apex; free basal portion markedly auriculate and extending across and beyond the stem; plants always sterile and with abundant discoid gemmae.
  - a. Plants of tropical and subtropical regions, growing only on living leaves of trees, shrubs, and herbs; dioicous; vegetative reproduction by means of large, circular, discoid gemmae.
- 5. *R. australis*
  - 6. *R. obconica*
  - 7. *R. complanata*
  - 8. *R. caloosiensis*
  - 9. *R. Langloisii*
  - 10. *R. andicola*
  - 11. *R. flaccida*

1. RADULA TENAX Lindberg, Acta Soc. Sci. Fenn. 10: 492.  
1875

*Radula pallens* Sulliv. Musci Alleg. 261. 1846. Not *R. pallens* (Sw.) Dum.

Plants dull green usually with a bronze cast: stems 1–6 cm. in length and 0.2 mm. in width, pinnately and in most cases bipinnately branched, the branches wide-spreading and arising at frequent intervals along the stem, separated by two to six leaves: stem leaves not overlapping on the older portions of the plant, subimbricate toward the growing tip, spreading from the stem at an angle of 80°, somewhat falcate, the keel straight or more

rarely slightly incurved or faintly arched; dorsal lobe  $1.4 \times 0.65$  mm., ovate, somewhat convex, the margin entire, apex rounded, the base free two-thirds its length, auriculate, arching across the stem, the line of attachment oblique on the axis; ventral lobe  $0.15 \times 0.1$  mm., quadrate, the apex somewhat obtusely angled, the base rounded, definitely auriculate, and extending from one-fourth to the entire distance across the stem; rhizoids infrequent, in most cases completely lacking; leaf cells with usually well defined trigones with straight or slightly bulging sides; cells of the leaf margin  $18 \times 15 \mu$ ; median cells  $23 \times 18 \mu$ ; basal cells  $23 \times 18 \mu$ ; leaves of the branches of the first order smaller, usually subimbricate, not at all falcate and obliquely spreading from the axis at an angle of  $60^\circ$ – $70^\circ$ ; the keel never straight or incurved but always slightly arched; dorsal lobe  $0.4 \times 0.3$  mm., ovate, the apex rounded; ventral lobe  $0.23 \times 0.15$  mm., subquadrate, frequently with rhizoids: dioicous: male inflorescence intercalary on a branch, less frequently terminal, of two to nine pairs of bracts, the bracts closely imbricate, much inflated at the base, the keel strongly arched; the dorsal lobe  $0.6 \times 0.4$  mm., usually erect, rounded at the tip and the base arching across and some distance beyond the axis; the ventral lobe  $0.4 \times 0.3$  mm., bluntly angled at the tip, its base partially free, auriculate, and arching nearly across the axis: female inflorescence terminal on the stem or a leading branch, usually with a single innovation, more rarely innovating on both sides, one innovation not developing beyond a bud, the other continuing the growth of the stem and pushing the female flower into a lateral position; female bracts wide spreading, usually becoming widely separated and often freely exposing the archegonia; dorsal lobe  $1 \times 0.6$  mm., narrowly ovate; ventral lobe  $0.4 \times 0.4$  mm., subquadrate, the base rounded into a pronounced auricle; perianth unknown.

TYPE LOCALITY: ad truncos emortuos in Marylandia et Carolina Superiore.

HABITAT AND DISTRIBUTION: in depressed, dense mats on moist rocks, less frequently on trunks of trees, in mountainous and hilly regions; throughout New England and southward to North Carolina.

ILLUSTRATIONS: Lorenz, A., *Bryologist* 11: *pl.* 2. 1908.

MAINE: Greenville, 1911, *Evans* (*Rhodora* 14: 17. 1912).—NEW HAMPSHIRE: Shelburne, 1883, *Farlow*; near Coösauk Falls, Mt. Madison, *Evans*, Crystal Cascade, White Mts., *Underwood & Cook*, *Hep. Amer.* 52; Franconia Notch, *Evans et al.*; the Pool, Franconia, *Farlow*; Waterville, A. Lorenz 75, *Evans*.—VERMONT: Granville Notch, 1916, *Weatherby* (Lorenz, A., *Bull. Vt.*

Bot. & Bird Club 3: 8. 1917); Birch Hill, Brandon, *Dutton* 1375, 1377.—MASSACHUSETTS: Chebocco Lake, Manchester, 1903, *Farlow*; Sheffield, *A. Lorenz*.—CONNECTICUT: Beacon Falls, 1890, *Evans*; Branford, Salisbury and Redding, *Evans*; Salisbury, *A. Lorenz* 269, *Nichols* (distributed in Haynes, Amer. Hep. 89); Redding, *C. C. Haynes* 896. Most of these localities are recorded by Evans and Nichols, Bull. Conn. Geol. & Nat.

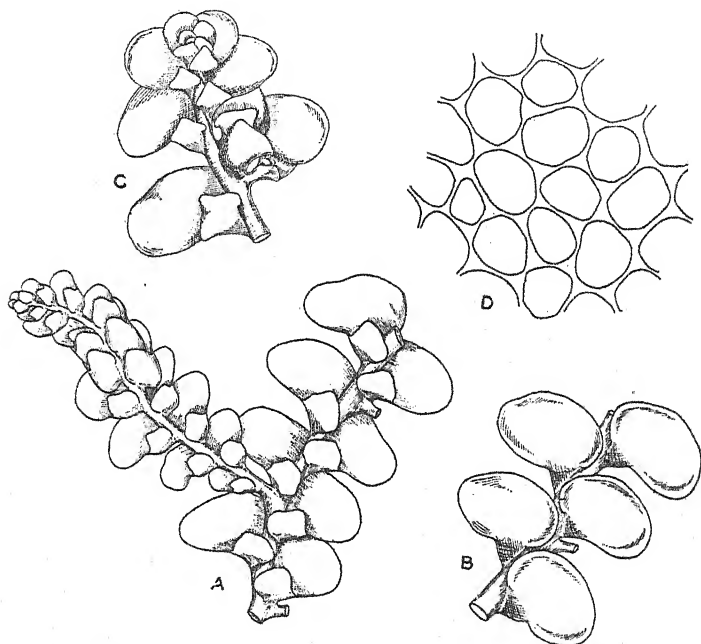


FIG. 1. *RADULA TENAX* Lindb. A. Portion of a male plant showing the intercalary male inflorescence, ventral view,  $\times 18$ . B. Portion of a sterile plant, dorsal view,  $\times 18$ . C. Portion of a female plant showing the pseudo-lateral female flower, ventral view,  $\times 18$ . D. Leaf cells showing thickenings at the cell angles,  $\times 450$ .

Hist. Surv. 11: 70. 1908.—NEW YORK: Onteora Mt., near Tannersville, 1891, *A. M. Vail* 5; Little Moose Lake, Herkimer Co., *C. C. Haynes* 1409.—MARYLAND: without definite locality, *Sullivant*, distributed (as *R. pallens*) in Musci Alleg. 261.—VIRGINIA: Nick's Creek, 1892, *E. G. Britton* 44; White Top Mt., *E. G. Britton* 6, 102; same locality, *Small* (distributed in Blue Ridge Hepatics, S. W. Virginia 61). These localities are re-

corded by Small & Vail, Mem. Torrey Club 4: 193. 1893.—WEST VIRGINIA: Tibbs Run, 1892, *Millsbaugh* (Bull. W. Va. Agr. Expt. Station 24: 495. 1892.); Fairview, *E. M. Fling*.—NORTH CAROLINA: without definite locality, *Sullivan*, distributed (as *R. pallens*) in Musci Alleg. 261; near Montreat, Buncombe Co., *Standley & Bollman* 10160 (H.). This species was also reported as collected by Atkinson in 1901 at two stations in the state (see Andrews, A. LeRoy, Bryologist 17: 59. 1914).—"On rocks and fallen trunks in mountainous regions," *Austin*, Hep. Bor. Am. 87 (as *R. pallens*).<sup>2</sup>

*Radula tenax* was described in 1875 by Lindberg from material which had been collected in Maryland and North Carolina and distributed as *R. pallens* (Sw.) Dumortier in Sullivan's Musci Alleghanienses 261. Although this material is to be regarded as the type, Lindberg also based his species on material collected in mountainous regions (no definite station) and issued by Austin in Hep. Bor. Am. 87, and on material collected in the Catskills, New York, in August 1868, by P. T. Cleve. Of the three collections the first two have been examined. The points of difference between these two species are the following: the branching in *R. tenax* is simply pinnate, while in *R. pallens* it is dichotomous; the leaves of *R. tenax* are elliptical-ovate, while those of *R. pallens* are round-ovate; the lobule of *R. tenax* is ovate and attached to the stem scarcely half the length of the base, while in *R. pallens* the lobule is trapezoidal and the base is fused more than half its length.

A study of this species reveals a considerable amount of variation in regard to several characters. The most marked variation probably is in connection with the trigones. Austin's material and also the majority of the specimens collected in the South show rather pronounced thickenings in the angles of the leaf cells. On the other hand much of the northern material shows an absence of trigones, although cell thickenings are conspicuous in some material as, for example, in the specimen from Sheffield, Mass. Although trigones are usually present in the southern material, they are not absolutely constant and may also

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<sup>2</sup> In this and the other lists of specimens examined "H." signifies the herbarium of Miss Caroline C. Haynes, and "N. Y." the herbarium of the New York Botanical Garden. The remaining specimens are in the herbarium of Yale University.

vary in degree. Material collected by E. M. Fling at Fairview, West Virginia, possesses leaf cells with extremely thin walls and no trigones. Very obviously the degree to which the cell angles may be thickened is so variable that it can possess no real specific value. In addition to this, in many cases, there is a marked difference in the general appearance between plants collected in the North and those from the southern limit of the range. Frequently in northern material the plants are less robust and have the appearance of the branches of the first order of the southern forms. This may possibly be interpreted as a juvenile condition beyond which many of the plants of more northern distribution are not able to pass.

*R. tenax* possesses no definite structures for vegetative propagation nor does this species shed its leaves. However, old portions of plants, which are almost in a state of disintegration, may produce abundantly at any location on the surface of the leaves small, tuberous outgrowths, which then give rise to leafy shoots.

2. *RADULA BOLANDERI* Gottsche; Stephani, Hedwigia 23:

145. 1884

*Radula spicata* Aust. Bull. Torrey Club 6: 19. 1875. Not *R. spicata* Mitt., 1862.

*Radula arctica* Steph. Bot. Jahrb. 8: 98. 1886.

Plants usually dark green, dull, often becoming yellowish green with age: stems 1-2 cm. in length and 0.09 mm. in width, somewhat regularly pinnately and bipinnately branched, the branches 1-5 mm. in length and 0.06 mm. in width, alternate, separated usually by two leaves of the stem and spreading obliquely at an angle of 70°-80°, frequently simple but more often with a few short branches of the secondary order: stem leaves scarcely imbricate, spreading from the stem obliquely at an angle of 60°-70°, the keel straight or more often slightly arched; the dorsal lobe 0.8 × 0.65 mm., ovate, decidedly convex, the base free about one-half its length, the free portion arching usually almost across the stem, the fused base attached to the stem by a straight line, the apex broadly rounded; the ventral lobe 0.45 × 0.35 mm., subquadrate, the base free about half its length, the free portion subauriculate, arching part way across the stem, the line of attachment oblique, the apex blunt and almost forming a right angle; rhizoids usually present on a somewhat inflated cushion at the base of the lobule; leaf cells comparatively thin-walled, usually with small thickenings at the angles; cells of the



margin of the dorsal lobe  $15 \times 11 \mu$ , cells of the median portion  $18 \times 14 \mu$ , cells of the base  $18 \times 15 \mu$ ; leaves of the branches of the first order slightly imbricate, obliquely spreading as those of the stem; the keel somewhat more arched; the dorsal lobe  $0.35 \times 0.3$  mm., ovate, convex; the ventral lobe as in the stem leaves,  $0.25 \times 0.2$  mm., usually with an inflated base bearing rhizoids; leaves of the axes of the second order subequally bilobed,  $0.15 \times 0.13$  mm.; the keel much arched; rhizoids absent; dioicous; the male inflorescence a long, slender, compact ament of two to thirty pairs of bracts, usually terminal on the stem or a branch of the first order, occasionally proliferating at the tip; the bracts much inflated at the base, subequally lobed,  $0.5 \times 0.35$  mm., the lobes rounded at the tip; rhizoids absent: female inflorescence terminal on the stem or a leading branch, usually innovating on one or both sides, the innovations in most cases not fertile and usually not longer than other branches of the first order, less frequently bearing female flowers and assuming stem-like growth; female bracts subequally bilobed, about the size of the stem leaves, the keel straight or slightly inwardly curved; the dorsal lobe  $0.85 \times 0.45$  mm., broadly rounded at the tip; the ventral lobe  $0.7 \times 0.45$  mm., rounded at the tip; perianth 1–2 mm. in length, tapering from a narrow base abruptly to a wide, shallowly two-lipped, faintly and coarsely undulate mouth, strongly flattened toward the free end: capsule oval-cylindrical; the outer layer of cells with strong, horizontal bands of thickening on all the vertical, radial walls, the thickenings often extending slightly over the outer tangential wall and separated or more rarely confluent; the inner layer of large, more irregular cells, thickened more or less uniformly on most of the radial walls, transverse bands of thickening on the tangential walls absent.

TYPE LOCALITY: California. Mendocino City, leg. Bolander.

HABITAT AND DISTRIBUTION: on moist rocks or on the bark of trees; frequent along the Pacific Coast of North America from California to Alaska.

ILLUSTRATIONS: Stephani, Bot. Jahrb. 8: pl. 3. f. 11. 1886; Pearson, W. H., Can. Hep. pl. 4. 1890.

ALASKA: Port Etches, 1892, *Underwood* 448 (H.); Ratz Harbor, *Frye* 297, 312 (Evans, A. W., Bull. Torrey Club 41: 606. 1914).—BRITISH COLUMBIA: Observatory Inlet, *Douglas* (N. Y.) no date given; Vancouver, *Pringle* 536 (N. Y.); Victoria, *Macoun* 17, 40, 107; Ucluelet, *Macoun* 22, 41, 43, 81, 113; Esquimalt, *Macoun* 30; Sidney, *Macoun* 41 (H.); Vancouver I., *Macoun* 13 (N. Y.), 17 (N. Y.); Comox, *Macoun* 82 (N. Y.); Goldstream, *Macoun* 18; Alert Bay, Vancouver I., *Dawson* (N. Y., Pearson, W. H.,

Can. Hep. 16, as *R. spicata*. 1890); Port Renfrew, *Skinner* 3; same locality, *G. Gibbs* 6, 50, 59, 110, 129, 168. Several of these localities are listed by Evans, A. W., *Postelsia* 1906: 230. 1906.—WASHINGTON: Seattle, 1891, *Piper* 20 (H.); Cathlamet, *Foster* 492, 492b (H.); Gate, *Foster* 1960, 2019 (H.); near Aberdeen, *Foster* 929 (H.), 945b (H.). Several of these localities are listed by Haynes, C. C., *Bryologist* 12: 69. 1909.—OREGON: Portland, 1888, *Underwood* (H.); Forest Grove, *Lloyd* (N. Y.); Silverton, *Foster* 1391 (H.), 1384 (H.); North Silver Creek,

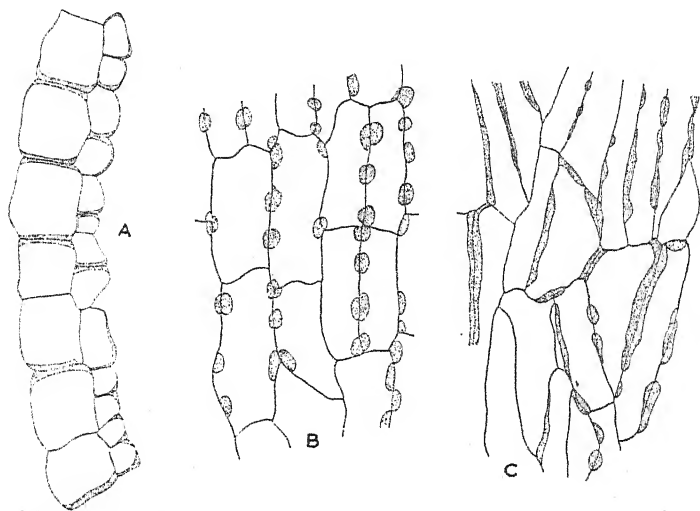


FIG. 2. *RADULA BOLANDERI* Gottsche. A. Cross-section of the capsule wall,  $\times 450$ . B. Outer layer of the capsule wall,  $\times 450$ . C. Inner layer of the capsule wall,  $\times 450$ .

Marion Co., *Foster* 1320 (H.). Austin's *R. spicata* was based in part on specimens from Salem, collected by E. Hall, but these specimens have not been available for examination.—CALIFORNIA: Mendocino City, *Bolander*, *Stephani* (N. Y.) TYPE; Muir Woods, *M. L. Campbell*; Lily Lake, *E. C. Suttcliffe* 33; Marin Co., *Underwood & Cook*, *Hep. Amer.* 32; Mill Valley, *Howe* 3; same locality, *Blasdale*, (H.); Marin Co., *M. Kean* 32 (H.); near Lake Lagunitas, *E. C. Suttcliffe* (H.); Mendocino, *Howe* 549 (N. Y.); near Felton, *Underwood* (H.); Cazadero, *Howe* (N. Y.); Eureka, *Howe* 918 (N. Y.); near McBride's, Mad River,

Humboldt Co., *Howe 1056* (N. Y.). M. A. Howe lists several of these localities in *Mem. Torrey Club* 7: 159. 1899.

Austin's *Radula spicata*, although published earlier than the *Radula Bolanderi* of Gottsche, is a homonym of *Radula spicata* Mitten, and accordingly untenable in spite of the fact that Mitten's species has been reduced to synonymy under *Radula formosa* (Meissn.) Nees by Stephani.

*Radula arctica* is here included as a synonym since there is nothing in Stephani's description or figure of this plant to set it apart from the juvenile condition of *R. Bolanderi*. This opinion was first expressed by M. A. Howe in his work on the hepatics of California (*Bull. Torrey Club* 7: 159. 1899). Stephani, however, maintains that the specimen is not juvenile but presents no further evidence to support his view.

*R. Bolanderi* agrees with *R. tenax* in several characteristics, such as the dioicous inflorescence and the entire absence of gemmae or of any tendency to shed its leaves. There is, however, no difficulty in separating the two species. Each species is characterized by a very definitely restricted geographical distribution. *R. Bolanderi* is known only along the Pacific Coast from California to Alaska. *R. tenax*, on the other hand, is restricted to the Atlantic Coast, being known from Maine to North Carolina. Pearson (*Can. Hep.* 1890) has reported *R. tenax* from Vancouver Island on the basis of material collected by Dawson at Alert Bay in 1885. This material, however, has been identified as *R. Bolanderi* by Evans (*Postelsia* 1906: 230. 1906).

The points of difference between these two species are sufficiently marked to make a distinction readily possible. In *R. Bolanderi* the leaves are more decidedly imbricate, less widely spreading and not at all falcate. When compared with *R. tenax* the lobule in *R. Bolanderi*, in relation to the lobe, is larger, not at all or only slightly auriculate and extends less across the stem. In fact, there is no other North American form which possesses the narrowly spreading, spoon-shaped leaves with large lobules which characterize *R. Bolanderi*. In regard to the sexual structures there are also striking differences. The male inflorescence of *R. Bolanderi* is in most cases terminal, the bracts densely imbricate and more compact than in the case of *R. tenax*. The female inflorescence of *R. Bolanderi*, with usually two innovations, is readily distinguished from the pseudo-

lateral female flower of *R. tenax* with its widely separated female bracts.

3. *RADULA POLYCLADA* Evans, Bull. Torrey Club 41: 607. 1915

Plants dull, yellowish green, becoming brown with age, 2-3 cm. in length, prostrate in loose mats: stems 0.2 mm. in width, profusely and regularly pinnately branched; branches 0.1 mm. in width, arising almost uniformly behind every leaf, widely spreading at an angle of  $90^{\circ}$ , 4-8 mm. in length, frequently bearing very short axes of the second order: stem leaves entire, somewhat imbricate, widely spreading at an angle of  $70^{\circ}$ - $80^{\circ}$ , and slightly falcate, the keel slightly arched; dorsal lobe of the stem leaves  $0.95 \times 0.65$  mm., broadly ovate, convex and often revolute at the tip, the apex broadly rounded, the base slightly auriculate and free for one-third the distance, arching only slightly over the stem and only slightly decurrent; ventral lobe  $0.4 \times 0.35$  mm., quadrate, appressed to the dorsal lobe, the base free about one-half its length, the free portion slightly auriculate at the point of fusion and arching only slightly over the stem, the free margin parallel to the keel, the apex obtusely angled, rhizoids entirely lacking; leaf cells plane, without definite trigones, occasionally somewhat thickened at the angles, the cuticle smooth, marginal cells  $15 \times 10 \mu$ , median cells  $22 \times 17 \mu$ , basal cells  $30 \times 25 \mu$ ; leaves of the primary axis more or less imbricate, dorsal lobe  $0.45 \times 0.35$  mm., ovate, convex, less widely spreading than the stem leaves, the ventral lobe  $0.2 \times 0.1$  mm., subquadrate, the free margin shorter than the keel; leaves of the secondary axes still less widely spreading, subequally bilobed: dioicous: female inflorescence terminal on a short branch of the first order, innovating at the base, the innovations two, more rarely one, and not fertile; female bracts large and wide spreading, the keel strongly incurved; dorsal lobe  $1.4 \times 0.8$  mm., narrowly ovate, rounded at the apex and somewhat convex; dorsal lobe  $0.85 \times 0.65$  mm., rounded at the apex and somewhat concave: perianth and male inflorescence not known.

TYPE LOCALITY: on rocks, Aats Bay, Alaska.

HABITAT AND DISTRIBUTION: on moist rocks and old logs; Alaska to Washington.

ILLUSTRATIONS: Bull. Torrey Club 41: figs. 2, 3. 1915.

ALASKA: Sitka, 1894, U. S. Fish Commission; Aats Bay, Frye 900, TYPE; Unalaska, Seitchell et al. 1025; Augustine Bay, Frye 580, 586, Foster 758; Ratz Harbor, Frye 312; Shipley Bay, Foster 788; Exchange Cove, Frye 260; Hidden Inlet, Frye 73; Prince of Wales Is., Foster 1123. Most of these are listed as

*R. Bolanderi* by Evans, A. W., Bull. Torrey Club 41: 606. 1915.—BRITISH COLUMBIA: Port Renfrew, 1901, *G. Gibbs* 59 (listed as *R. Bolanderi* by Evans, A. W., *Postelsia* 1906: 230. 1906.); Ucluelet, *Macoun* 43, 81, 113 (listed as *R. Bolanderi*).—WASHINGTON: near Olympic Hot Springs, Clallam Co., 1914, *Foster* 2826.

Compared with other North American species of *Radula* of the group in which gemmae are absent and in which there is no tendency to shed the dorsal lobe, *R. polyclada* most closely resembles *R. Bolanderi* and has often been confused with it as the

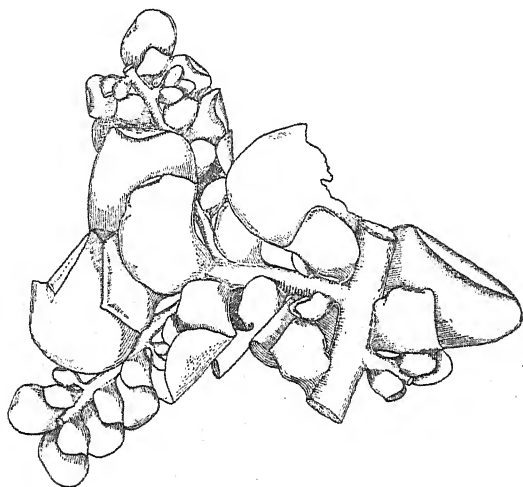


FIG. 3. *RADULA POLYCLADA* EVANS. Portion of a female plant showing the female inflorescence terminal on a short branch of the first order with two sub-floral innovations, ventral view,  $\times 18$ .

list of specimens indicates. Both species are restricted to the Pacific Coast region and, of the two, *R. polyclada* has the more northern range. In regard to the female inflorescence, size, and mode of branching, however, the two are strikingly different. *R. polyclada* is always larger and more regular in its branching habit. Moreover, in this species the leaves spread more widely from the stem, rhizoids are always entirely lacking and the apex of the lobule is less acutely angled. The most marked difference between these two species exists in connection with the female inflorescence. In *R. polyclada* the female flowers are always terminal on a short branch of the first order and

never at the apex of the stem or a leading branch as is the case in *R. Bolanderi*. The female bracts are somewhat larger than the stem leaves and more widely spreading while in *R. Bolanderi* they do not exceed the leaves of the stem in size and are more erect.

A decidedly more striking agreement exists between *R. polyclada* and the Siberian species, *R. prolifera* Arnell, known only from the type specimen, which was collected by H. Nilsson Ehle in 1898 at Bulkur, in the valley of the Lena.<sup>3</sup> The points of similarity and difference have been well brought out by Dr. Evans in his paper on the Alaskan Hepaticae<sup>4</sup> and need not be repeated here.

#### 4. RADULA SULLIVANTII Austin, Bull. Torrey Club 6: 19.

1875

Plants dull green, often with a golden yellow cast: stems 1-2 cm. in length and 0.15 mm. in width, rather profusely branched, pinnate and frequently bipinnate, the branches 1-3 mm. in length and 0.08 mm. in width, more or less wide spreading at first but later approaching the stem: leaves of the stem subimbricate, strongly falcate, wide spreading from the stem at an angle of 90°, the keel usually definitely arched; dorsal lobe 0.7 × 0.6 mm., broadly ovate, rounding out abruptly beyond the keel, the apex broadly rounded, the base free about half its length, not at all auriculate and usually spreading only a little over the stem, the line of attachment straight; ventral lobe 0.35 × 0.25 mm., rhomboidal, the outer margin straight, the anterior margin shorter than the keel, the apex obtuse, the base fused to the stem practically its entire length, a pronounced mammilliform swelling at the base of the lobule usually without rhizoids: leaves of the branches of the first order essentially like those of the stem; the dorsal lobe 0.55 × 0.4 mm., the base slightly auriculate; ventral lobe 0.35 × 0.2 mm., mammilliform outgrowth usually present: cells of the leaf usually thick-walled, often with distinct trigones; marginal cells 16 × 14 μ, median cells 17 × 14 μ, basal cells 17 × 14 μ: dioicous: the male inflorescence usually intercalary on the stem or a branch, rarely terminal, of two to four pairs of bracts, subimbricate, the keel strongly arched, the dorsal lobe 0.55 × 0.4 mm.; ventral lobe 0.4 × 0.2 mm., without rhizoid-bearing inflation: female inflorescence not known: vegetative propagation by means of caducous vegetative leaves, which occasionally give rise to thaloid growth before shedding.

<sup>3</sup> Ark. för Botanik 13: 12. pl. 1. f. 1, 2. 1913.

<sup>4</sup> Bull. Torrey Club 41: 609. 1915.

TYPE LOCALITY: mountains of Georgia, *Sullivan, Lesquereux*.

HABITAT AND DISTRIBUTION: in depressed, dense mats on moist rocks and banks; known from Georgia and Alabama.

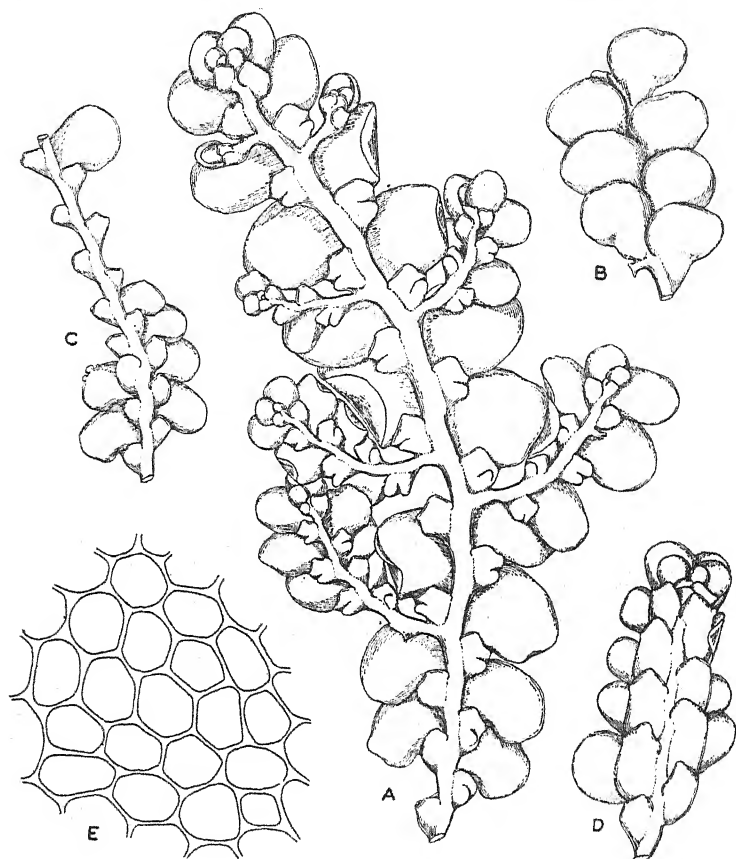


FIG. 4. *RADULA SULLIVANTII* Austin. A. Portion of a sterile plant, ventral view,  $\times 18$ . B. Portion of the same, dorsal view,  $\times 18$ . C. Portion of a sterile plant after shedding the dorsal lobes (Bruchblätter), ventral view,  $\times 18$ . D. Portion of a male plant showing a terminal male inflorescence, ventral view,  $\times 18$ . E. Leaf cells,  $\times 450$ .

GEORGIA: without definite locality, 1843, *Sullivan & Lesquereux*, TYPE (distributed in Austin's Hep. Bor. Am. 88<sup>c</sup>); Tallulah Falls, *Underwood* (distributed in Hep. Amer. 105), *Small* 90, 9181; *Seymour*, Estotoah Falls, *Small* (distributed in Hep. E. N. Amer. 15).—ALABAMA: Fairhope, 1924, *Evans*.

This species belongs to a group which is characterized by a more or less pronounced tendency on the part of the leaves to shed their dorsal lobes, and *R. Sullivantii* has this tendency to a marked degree. The lobes are, in fact, Bruchblätter, which first give rise to flat, thalloid outgrowths from the lobe margin and then these develop into leafy shoots. Occasionally these thalloid bodies develop prematurely on the margin of a lobe before shedding. Under these circumstances they sometimes simulate gemmae, except for the fact that they do not separate from the lobes.

*R. Sullivantii* agrees with the preceding forms in its lack of discoid gemmae. It is, however, easily set apart from these by the presence of Bruchblätter, its strongly falcate leaves, and the fact that the base of the lobule is attached practically its entire length.

#### 5. RADULA AUSTRALIS Austin, Bot. Gaz. 1: 32. 1876

Plants green, often with a tinge of brown: stems 1.5–3 cm. in length and 0.15 mm. in width, somewhat irregularly pinnately branched, the branches wide spreading at first and forming an angle of about  $70^\circ$  with the stem, later approaching the stem, frequently bearing a few scattered branches of the second order: stem leaves with a more or less marked tendency to shed the dorsal lobe, subimbricate, spreading from the stem at an angle of about  $70^\circ$ , falcate, the keel straight or slightly incurved; the dorsal lobe  $1.5 \times 1$  mm., ovate or somewhat obovate, the apex broadly rounded, the base free about half its length, the free portion auriculate and arching across the stem and frequently beyond, the line of attachment oblique; ventral lobe  $0.55 \times 0.55$  mm., subquadrate, somewhat appressed to the dorsal lobe toward the apex, the anterior margin curved and occasionally with a fold in the region of the apex, the apex blunt but not broadly rounded, the base free usually about one-half its length, the free portion auriculate and extending from one-half to wholly across the stem, the line of attachment curved, a small rhizoid-bearing inflation usually present toward the base of the lobule: cells of the leaf thin-walled throughout; cells of the marginal portion  $18 \times 20 \mu$ , cells of the median portion  $20 \times 22 \mu$ , cells of the base  $21 \times 29 \mu$ : leaves of the branches of the first order slightly different; the dorsal lobe  $0.9 \times 0.65$  mm., narrower and usually more decidedly falcate than that of the stem leaf; the ventral lobe  $0.3 \times 0.25$  mm., the anterior margin less broadly rounded, rhizoids only occasionally present; leaves of the branches of the second order essentially like those of the other branches but proportionately smaller: dioicous: male inflores-



cence intercalary on the main axis and the branches of the first and second orders, often appearing terminal due to the only slight vegetative growth at the tip; bracts in three to ten pairs, imbricate, much inflated toward the base, the keel strongly arched; dorsal lobe  $0.55 \times 0.25$  mm., usually erect and rounded at the apex; ventral lobe  $0.5 \times 0.25$  mm., the apex narrowly rounded: female inflorescence terminal on the stem or a branch, innovating on both sides, one innovation rarely developing beyond a rudimentary bud, the other often continuing the growth of the stem or other axis and frequently fertile; bracts erect; the dorsal lobe  $0.85 \times 0.45$  mm., broadly rounded at the apex; ventral lobe  $0.55 \times 0.3$  mm., obtusely angled at the tip; perianths 1–2 mm. long, cylindrical below, flattened above, shallowly two-lipped, the lips rather regularly and definitely undulate: capsule oval-cylindrical; the outer layer composed of regular, more or less isodiametric cells, square or broadly rectangular in cross-section, thickenings present on the vertical radial walls of certain cells occurring in definite sequence: median line of each valve formed by thin walls, three vertical lines on either side of more or less uniformly thickened walls, the next vertical line of thin walls, the next vertical line of uniformly thickened walls and the remaining two or three lines thin-walled throughout; inner layer of cells with horizontal bands of thickening on most of the vertical radial walls extending usually across the inner tangential wall: vegetative reproduction by means of caducous leaves.

TYPE LOCALITY: near Augusta, Georgia, *Sullivan*, 1845.<sup>5</sup>

HABITAT AND DISTRIBUTION: in dense depressed mats, frequently growing mixed with mosses or on the bark of trees; known from Georgia, Florida, Louisiana, Cuba and the Bahama Islands.

FLORIDA: without definite location, *Chapman* 49 (N. Y.); Gainesville, *Wade & Robinson*; Blandton, *Underwood* (H.); Sanford, *Rapp* 4 (H.), 24, 40 (H.) (Haynes, C. C., *Bryologist* 18: 20. 1915); various hammocks in Dade Co., *Small et al.* 1377, 1403, 1414, 1432, 1530, 1538, 2817, 2824, 3689, 5234, 5238, 5239, 5249, 5265, 5288, 5296, 5300, 5302, 6145, 6147, 6154, 6156, 6157, 6177, 6183, 6212, 6213, 6224, 6225, 6231, 6237, 7010, 7022, 7023, 7028, 7032, 7040; Florida Keys, *Small et al.* 1524, 1526, 1535, 1548, 1554, 3663, 7819.—LOUISIANA: Bois Lobbé, 1891, *Langlois* (H.); Keystone, *Langlois* (H.).—CUBA: vicinity of San Diego de los Baños, Province of Pinar del Rio, 1915, *Brother Leon* 5232b.—BAHAMA ISLANDS: without definite location, *Northrop* 349; Maidenhead Coppice, New Providence,

<sup>5</sup> The type of *R. australis* has not been examined.

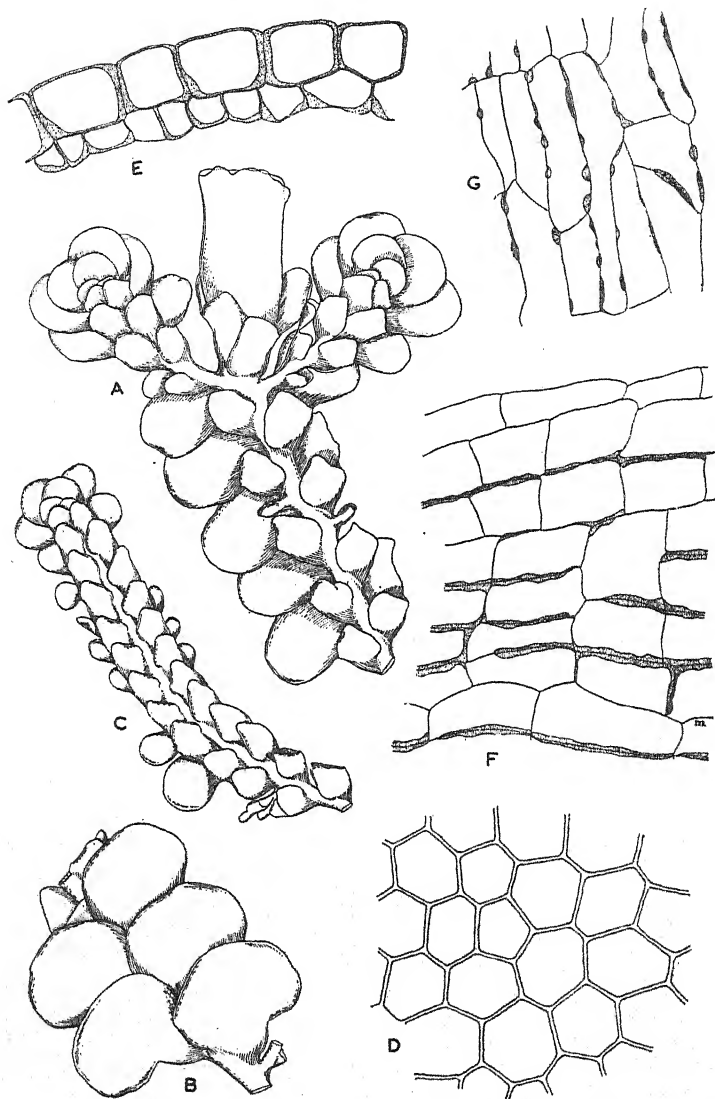


FIG. 5. *RADULA AUSTRALIS* Austin. A. Portion of a female plant showing the terminal flower with the two sub-floral innovations and mature perianth, ventral view,  $\times 18$ . B. Portion of a sterile plant, dorsal view,  $\times 18$ . C. Portion of a male plant showing the amentiform male inflorescence, ventral view,  $\times 18$ . D. Leaf cells,  $\times 450$ . E. Cross-section of the capsule wall,  $\times 450$ . F. Outer layer of the capsule wall showing the median longitudinal line of the valve at M,  $\times 450$ . G. Inner layer of the capsule wall,  $\times 450$ .

*E. G. Britton* 3261, Nicholl's Town, Andros, *Brace* 6880 (Evans, A. W., Bull. Torrey Club 38: 206. 1911).

Austin in his original account of this species compares it with *R. pallens*. He shows that *R. pallens* differs, however, in being a much larger species in which the branching is never regularly pinnate but usually presents a dichotomous appearance. In regard to the male inflorescence he adds, in comparison, that the ament of *R. pallens* is much longer and never terminal. The last point is not actually a difference, as in none of the specimens of *R. australis* examined has the male inflorescence been found to be strictly terminal. It is always intercalary and in every case, when it appears to be terminal, close inspection shows proliferation at the tip. The leaves, moreover, when compared with those of *R. pallens* are more distinctly falcate, the lobule is larger and more acute, and the perianth is usually less elongate.

According to the treatment of North American species given here, *R. australis* belongs in the group in which gemmae are lacking and in which vegetative propagation is accomplished by caducous leaves. Of the forms within this group it most nearly resembles *R. Sullivantii* on account of its strongly falcate leaves. *R. australis* differs from *R. Sullivantii*, however, in several characters. It is usually a larger and more robust form with a less marked tendency to shed the dorsal lobe. The dorsal lobe usually extends across and beyond the stem and the base of the lobule is always free one-third to one-half its length. Furthermore, the male inflorescence of *R. australis*, with only slight proliferation at the tip, often appears to be terminal while in *R. Sullivantii* it is usually more obviously intercalary.

6. RADULA OBCONICA Sullivant, Gray's Manual, Ed. 1:  
688. 1848

Plants dull, olive green, occasionally tinged with yellow: stems usually not more than 1 cm. in length and about 0.15 mm. in width, rather indefinitely pinnately branched, the branches spreading at an angle of 80-90°, approaching the main axis above, separated by one to six leaves: stem leaves, except toward the tip, scarcely at all imbricate, spreading at an angle of 80°, slightly falcate, the keel slightly arched, straight, or more rarely slightly incurved; dorsal lobe 0.7 × 0.6 mm., ovate, convex, the apex broadly rounded, the base free one-third its length, the free portion subauriculate and arching only a short distance

over the stem, the line of attachment straight; ventral lobe  $0.25 \times 0.25$  mm., subquadrate, the outer margin parallel to the stem, the apex narrowed into a blunt tip, the base fused to the stem one-third to one-half its length, the free portion not auriculate, the attachment straight, rhizoids present on a more or less pronounced inflation: leaves of the branches of the first order essentially like those of the stem; the dorsal lobe  $0.45 \times 0.4$  mm., not at all falcate and slightly less widely spreading compared to the dorsal lobe of the stem-leaf; ventral lobe  $0.2 \times 0.2$  mm.: leaves of the branches of the second order with relatively smaller lobes, about  $0.2 \times 0.1$  mm.: cells of the leaf thin-walled and without trigones; marginal cells  $16 \times 13 \mu$ , median cells  $16 \times 13 \mu$ , basal cells  $19 \times 15 \mu$ : heteroicous: male inflorescence a series of several pairs of bracts on the main axis below the female flower, or intercalary on a branch or subfloral innovation, the bracts smaller than the leaves, imbricate, with a strongly arched keel; dorsal lobe  $0.45 \times 0.25$  mm., erect, rounded at the apex; ventral lobe  $0.35 \times 0.25$  mm., the apex blunt, without rhizoids: female inflorescence terminal on the stem or a branch, with usually two innovations, the innovations wide spreading and frequently fertile; the bracts erect, scarcely smaller than the leaves; dorsal lobe  $0.6 \times 0.45$  mm., ovate, the apex broadly rounded; the ventral lobe  $0.35 \times 0.25$  mm., the apex narrowly rounded: perianth clavate, 2-2.5 mm. in length by 1 mm. in width, the mouth becoming slightly constricted at maturity; shallowly two-lipped, the lips entire; cells of the outer wall of the capsule with pronounced horizontal bands of thickening on the radial walls extending in some cases somewhat over the inner tangential wall, pronounced thickenings on the inner tangential wall usually only at the ends of cells; cells of the inner layer large, irregular, the radial walls sometimes thin but frequently more or less uniformly thickened, the outer tangential walls scarcely thickened but usually more or less pigmented with yellow, except for scattered unpigmented areas: vegetative reproduction by means of caducous leaves.

TYPE LOCALITY: in cedrinis palustribus prope Urbana Ohionis; arborea.

DISTRIBUTION AND HABITAT: on moist rocks and tree trunks, not a common species, known in all the Atlantic Coast States from Maine to Georgia, also in Ohio, Wisconsin, Minnesota and Arkansas.

ILLUSTRATIONS: Gray's Manual, Ed. 2, *pl.* 8. 1856, and Bryologist 21: 59. *pl.* 25. 1918.

MAINE: Mt. Desert, Seal Harbor and Pemetic Mt., 1920, A. Lorenz (Rhodora 26: 12. 1924).—VERMONT: Salisbury, 1911, A. Lorenz (Bryologist 21: 57. 1918).—MASSACHUSETTS:

Sheffield, 1916, *A. Lorenz* (Bryologist 21: 57. 1918).—CONNECTICUT: Hamden, 1918, *Evans*; North Branford, Huntington, Kent, Redding, North Stonington, *Evans*; Killingworth, Southington, *Nichols*, Watertown, Southington, East Haddam, *A. Lorenz*; Oxford, *Harger*. Many of these localities are listed by

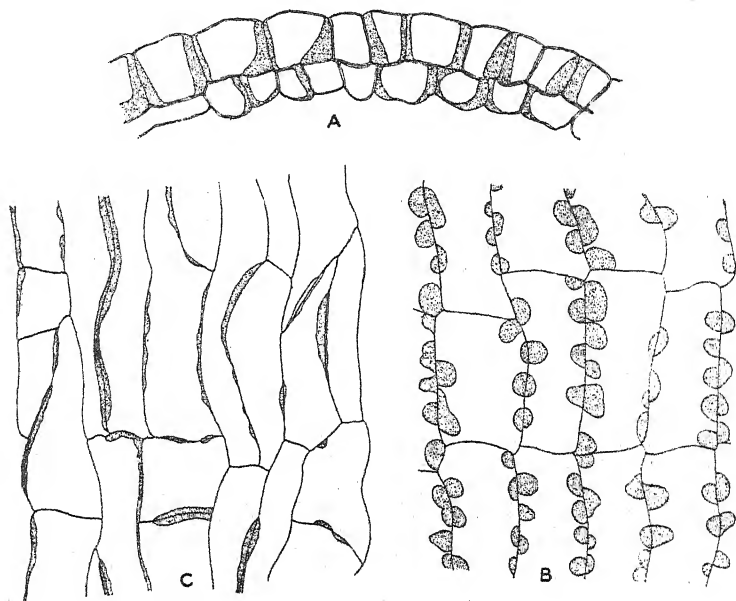


FIG. 6. *RADULA OBCONICA* Sull. A. Cross-section of the capsule wall,  $\times 450$ . B. Outer layer of the capsule wall,  $\times 450$ . C. Inner layer of the capsule wall,  $\times 450$ .

*A. Lorenz*, Bryologist 21: 57. 1918; and by *Evans & Nichols*, Bull. Conn. Geol. & Nat. Hist. Surv. 11: 70. 1908.—NEW YORK: Ithaca, 1887, *Coville* (H.).—NEW JERSEY: without definite locality, *Sullivan* 88.—PENNSYLVANIA: Delaware Water Gap, 1871, *Garber* (*Lorenz, A.*, Bryologist 21: 57. 1918).—DISTRICT OF COLUMBIA: Rock Creek Park, 1889, *Waite* 397 (H.); reported also from the same locality by *Holzinger* (Bryologist 10: 92. 1907); Broad Branch, *Waite* 520 (H.); Blogden's Mill, *Waite* H6 (H.); without definite locality, *Holzinger* (*Lorenz, A.*, Bryologist 21: 57. 1918).—VIRGINIA: Spout Run, 1889, *Waite* 488 (H.), 490 (H.); Nick's Creek, *E. G. Britton & A. M. Vail* 45 (*Lorenz, A.*, Bryologist 21: 57. 1918; and *Small & Vail*, Mem. Torrey Club 4: 193.

1893).—WEST VIRGINIA: Lick Run, 1909, *Sheldon* 3970; Burnt House, Randall, Albright, Marilla, *Sheldon* 4228 (H.), 4237, 4004 (H.).—NORTH CAROLINA: Montreat, 1913, *Standley & Bollman* 10160 (H.) (Standley, P. C., *Bryologist* 17: 71. 1914); Winston-Salem, *Chapman* 1056, 1176, 1773, 1073, 1673. This species was also collected by Atkinson in 1901 at several stations in N. C. See Andrews, A. LeRoy, *Bryologist* 17: 59. 1914.—GEORGIA: Tallulah, 1887, *Underwood & Cook*, Hep. Amer. 97; same locality, *Underwood* (H.), *Seymour* (Lorenz, A., *Bryologist* 21: 57. 1918).—OHIO: near Urbana, 1845, *Sullivant*, Musc. Alleg. 260 (N. Y.), TYPE; White's Gulch, Jackson Co., *Mrs. Bayard Taylor*.—WISCONSIN: Douglas Co., 1923, *Conklin* 1965 (H.).—MINNESOTA: Cook Co., 1911, *Conklin* 1135 (H.).—ARKANSAS: Swain, 1915, *Emig* 1071 (Lorenz, A., *Bryologist* 21: 57. 1918).

*R. obconica* agrees with all the preceding forms in its lack of true discoid gemmae. The tendency to shed the dorsal lobe exhibited by this plant shows more or less close relationship to *R. Sullivantii* and *R. australis*. It differs from these two species, however, in its heteroicous inflorescence and slightly falcate leaves. The mode of germination of the caducous leaves or Bruchblätter has been carefully followed by Miss Lorenz in her account of the species<sup>6</sup> and differs somewhat from that observed in the case of *R. Sullivantii*. After separation the lobe gives rise to small, massive, thalloid bodies along the margin which, after a few divisions, produce leafy shoots and ultimately new plants. The Bruchblätter of *R. Sullivantii*, on the other hand, give rise first to flat, thalloid bodies which soon produce the new plants.

# 7. RADULA COMPLANATA (L.) Dumortier, Comm. Bot. 112.

1822

*Jungermannia complanata* L. Sp. Pl. 1133. 1753.

*Martinellius complanatus* S. F. Gray, Nat. Arr. Brit. Pl. 1: 691. 1821.

*Radula alpestris* Lindb.; Berggren, Bidrag till Skand. Bryol. 29. 1866.

*Radula Hallii* Aust. Bull. Torrey Bot. Club 6: 19. 1875.

*Radula Notarisii* Steph. Hedwigia 23: 129. 1884.

*Radula Krausei* Steph. Bot. Jahrb. 8: 97. 1896.

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<sup>6</sup> Lorenz, A., *Bryologist* 21: 58. 1918.

*Stephanina complanata* O. Kuntze, Rev. Gen. Pl. 839. 1891.

*Stephanina alpestris* O. Kuntze, *l. c.*

Plants pale to bright yellow green: stems 1-2 cm. in length and 0.15 mm. in width, irregularly once or twice pinnate, the branches 1-2 mm. in length and 0.1 mm. in width, few in number, spreading at an angle of 80°: stem leaves densely imbricate, the keel slightly arched, wide spreading and very slightly falcate; dorsal lobe  $1.05 \times 0.85$  mm., broadly ovate, more or less convex, the apex broadly rounded, the base free about half its length, the free portion arching across the stem and usually beyond forming a definite auricle at the point of fusion with the stem, the line of attachment only slightly curved; ventral lobe  $0.45 \times 0.35$  mm., quadrate, appressed to the dorsal lobe, the apex rounded or obtusely angled, rarely slightly prolonged into a blunt tip, the base free one-half to one-third its length, slightly auriculate at the point of fusion with the stem, the line of attachment straight, rhizoid-bearing cushion usually present near the base: leaves of the branches of the first order essentially like those of the stem; the dorsal lobe  $0.6 \times 0.4$  mm. usually more erect and not at all falcate: ventral lobe  $0.2 \times 0.25$  mm., rhizoids present: cells of the leaf comparatively thin-walled, occasionally slightly thickened at the angles; cells of the margin  $22 \times 15 \mu$ , median cells  $20 \times 18 \mu$ , and basal cells  $22 \times 19 \mu$ : inflorescence paroicous: female inflorescence terminal on the stem or a leading branch, usually innovating at the base, the innovations rarely two, wide spreading and frequently fertile, the bracts erect with unequal lobes; dorsal lobe  $1.2 \times 0.9$  mm., the apex broadly rounded; ventral lobe  $0.75 \times 0.4$  mm.: male inflorescence a series of two to four pairs of bracts, imbricate, the keel strongly arched; dorsal lobe  $0.9 \times 0.75$  mm. broadly ovate, the base free about half its length, auriculate and arching nearly across the stem; ventral lobe  $0.55 \times 0.45$  mm., subquadrate, the apex obtusely angled, the base free one-half its length, auriculate: perianth 1.5-2.5 mm. in length, obconical, strongly flattened above, the mouth truncate, obscurely 2-lipped, the lips slightly obscurely repand: vegetative propagation by means of discoid gemmae frequent on the dorsal lobes of leaves, male and female bracts: outer layer of cells of the capsule wall composed of more or less regular rectangular cells with pronounced bands of thickening on alternate radial walls, the thickenings heavier toward the outer surface and varying considerably in height: cells of the inner layer irregular, thin-walled with no visible thickenings on the radial walls, reinforced with delicate horizontal bands on the inner tangential walls, usually 5-8 bands in each cell.

TYPE LOCALITY: in Europa ad arborum truncos.

HABITAT AND DISTRIBUTION: common on bases of trees and

on rocks in somewhat damp and well sheltered places; known practically throughout North America, Europe, Northern Asia, and Northern Africa.

ILLUSTRATIONS: Hooker, *Brit. Jung. pl.* 81. 1816; Macvicar, *Student's Handbook of British Hepatics* 387. 1912; Müller; Rabenhorst's *Kryptogamen-Flora* 6<sup>2</sup>: f. 158. 1912-16.

In view of the fact that *Radula complanata* is so well known, it has been considered unnecessary to list definite stations for this species. The collection of *Radulae* in the herbarium of Yale University contains 170 specimens of *Radula complanata*

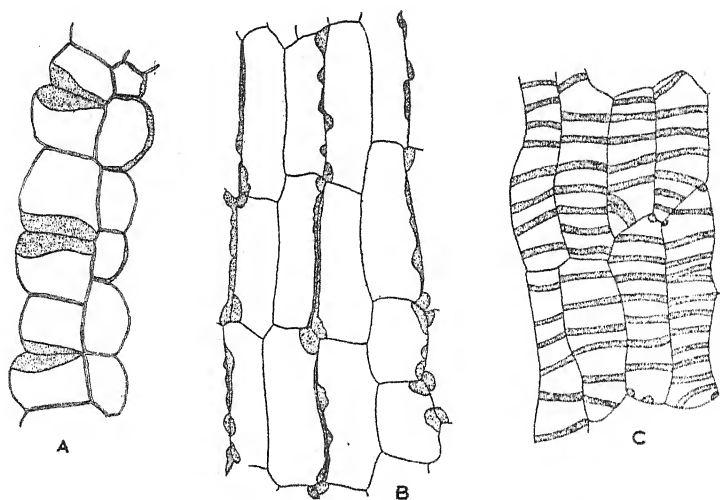


FIG. 7. *RADULA COMPLANATA* (L.) Dumort. A. Cross-section of the capsule wall,  $\times 450$ . B. Outer layer of the capsule wall,  $\times 450$ . C. Inner layer of the capsule wall showing transverse striae on the inner tangential walls,  $\times 450$ .

from Alaska, Canada, Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, Connecticut, New York, New Jersey, Pennsylvania, Maryland, Virginia, West Virginia, North Carolina, Florida, Louisiana, Michigan, Wisconsin, Minnesota, Montana, Colorado, Idaho, Arizona, Washington, Oregon, and California.

Two American forms, *R. Hallii* Austin and *R. Krausei* Stephani which have been proposed as new, are here included in the list of synonyms. *R. Hallii*, based on material collected



by E. Hall in Oregon, was said to differ in the following points: the leaf apices more incurved, involucre bracts smaller and more equally bilobed, and the perianth larger with several other minor differences. However, the type which is in the herbarium of the New York Botanical Garden, has been examined and reveals none of these differences sufficiently marked to warrant the recognition of a new species. On the other hand, the Alaskan type of *R. Krausei* has not been seen, yet material collected by Leiberg in Idaho and determined by Stephani as *R. Krausei* exhibits only the slight variations which may well come within the limits of variation of the recognized concept of this species. This view has also been expressed by M. A. Howe.<sup>7</sup>

*Radula complanata* has the distinction of being the earliest recognized member of the genus. In vegetative features it somewhat resembles *R. obconica*, but tends to be more robust. The absence of any tendency to shed the dorsal lobe, together with the presence of numerous discoid gemmae, at once sets these two species apart. In addition to this, the inflorescence of *R. complanata* is almost without exception paroicous, while in *R. obconica*, our only other monoicous species, male and female branches occur in addition to the bisexual branches. Since *R. complanata* usually fruits, the disposition of the sexual structures is a character which in the majority of cases can be conveniently employed.

The species most closely related to *R. complanata* is the European *R. Lindbergiana* Gottsche. In fact, these two species can be separated only on the nature of the inflorescence, which is dioicous in *R. Lindbergiana*. In this latter species, even when not actually in fruit, sterile archegonia may be found at the apices of the stems or branches, and the swollen, subinvolucral, male bracts, present in the paroicous *R. complanata*, are entirely lacking. Both Schiffner<sup>8</sup> and Jack,<sup>9</sup> who have made critical studies of *R. complanata* in Europe, have described plants in which are combined both the paroicous and heteroicous arrangements of the sexual structures. With this condition existing it would be impossible to assign with any certainty a single isolated female branch of a plant to either *R. complanata* or *R. Lind-*

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<sup>7</sup> Mem. Torrey Bot. Club 7: 160. 1899.

<sup>8</sup> Schiffner, V. Lotos 60: 72. 1912.

<sup>9</sup> Jack, J. B. Flora 64: 357. 1881.

*bergiana*. However, up to the present time, no heteroicous individuals of *R. complanata* have been noted in America. In fact careful inspection of all the North American material of *R. complanata*, which has been available, has failed to disclose any plants in which the inflorescence is other than paroicous. Therefore, it may be assumed from the evidence at hand that *R. Lindbergiana* is strictly an Old World species and does not occur in this country.

8. *RADULA CALOOSIENSIS* Austin, Bull. Torrey Club 6: 301.

1879

Plants yellow green: stems 1-1.5 cm. in length and 0.1 mm. in width, somewhat irregularly branched, the branches 1-5 mm. in length and 0.06 mm. in width, at first wide spreading and forming an angle of 80-90°, later approaching the axis, separated by two to four leaves: stem leaves spreading at an angle of 60°, somewhat densely imbricate, the keel slightly arched; dorsal lobe  $0.95 \times 0.7$  mm., broadly ovate, the apex broadly rounded, the base free one-third to one-half its length, the free portion auriculate and arching across and slightly beyond the stem, the line of attachment slightly curved; the ventral lobe  $0.35 \times 0.3$  mm., subquadrate, flat and appressed to the dorsal lobe, the terminal portion somewhat prolonged into a more or less acute tip, the base free about one-third its length, the free portion slightly auriculate and extending a short distance across the stem, the line of attachment oblique; rhizoids usually present on an inflated cushion near the base of the lobule: leaf cells uniformly thin-walled; cells of the leaf margin  $15 \times 13 \mu$ , cells of the median portion  $20 \times 18 \mu$ , cells of the leaf base  $33 \times 20 \mu$ ; leaves of the axis of the first order essentially like those of the stem, the keel slightly more arched; the dorsal lobe  $0.8 \times 0.65$  mm., the ventral lobe  $0.3 \times 0.3$  mm.; leaves of the axis of the second order proportionately smaller and less widely spreading: dioicous: male inflorescence terminal on a branch, apparently not proliferating, consisting of two or three pairs of densely imbricated bracts, the individual bracts much inflated at the base; the dorsal lobe  $0.7 \times 0.45$  mm., erect, rounded at the apex; the ventral lobe  $0.5 \times 0.25$  mm., the apex subacute: female inflorescence terminal on the stem or a subfloral innovation; bracts smaller than the leaves; the dorsal lobe  $0.7 \times 0.55$  mm., erect, broadly rounded at the tip; the ventral lobe  $0.4 \times 0.25$  mm., erect, rounded at the apex: perianths not seen: discoid gemmae abundant on the dorsal lobes of the stem and branch leaves, as well as on the male and female bracts.

TYPE LOCALITY: Caloosa, Florida, March, 1878.

HABITAT AND DISTRIBUTION: growing closely appressed to the bark of trees: known at present from three stations in Florida, two in Alabama and one in Louisiana.

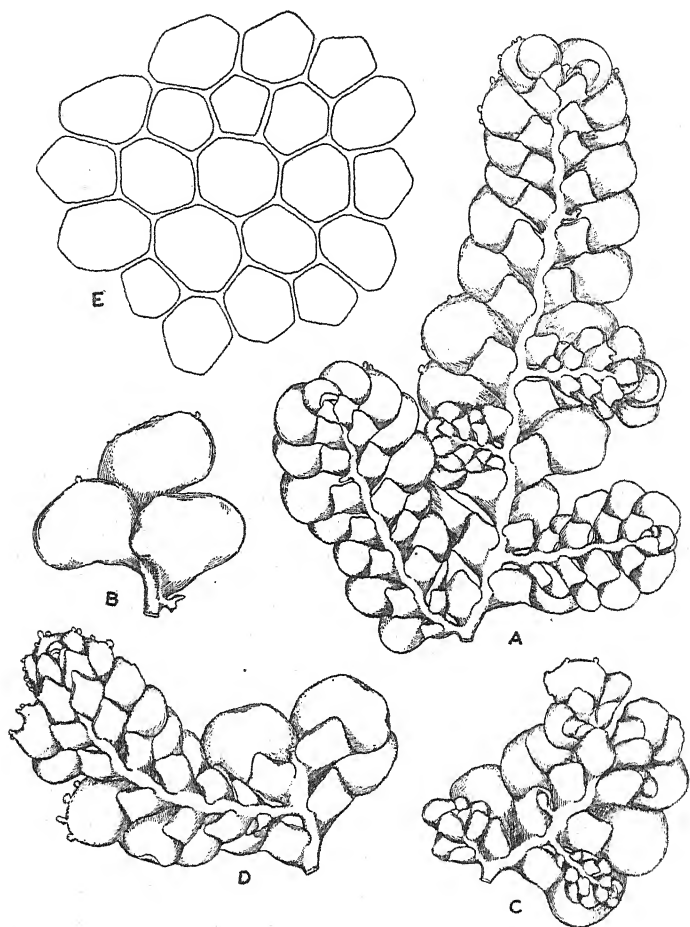


FIG. 8. *RADULA CALOOSIENSIS* Austin. A. Terminal portion of a sterile plant showing discoid gemmae on the margins of the dorsal lobes, ventral view,  $\times 18$ . B. Portion of the same, dorsal view,  $\times 18$ . C. Portion of a female plant showing the terminal flower with two sub-floral innovations, ventral view,  $\times 18$ . D. Portion of a male plant showing the terminal male inflorescence, ventral view,  $\times 18$ . E. Leaf cells,  $\times 450$ .

FLORIDA: Caloosa, 1878, *Austin*, TYPE; Blandton, *Underwood* 223; Sanford, *Rapp* 72 (H.), 86.—ALABAMA: near Fort Payne, 1905, *Harper* (N. Y.); Fairhope, *Evans*.—LOUISIANA: Bois Lobbé, 1890, *Langlois* (H.).

*R. caloosiensis* was considered a distinct species until 1910 when Stephani, in his synopsis of the genus,<sup>10</sup> reduced it to synonymy with *R. australis*. Although *R. caloosiensis* has without doubt, some characters in common with *R. australis*, there are several points of distinct difference which form sufficient basis for re-establishing the species. *R. caloosiensis* usually bears abundant discoid gemmae, its leaves are not at all falcate, and the lobe is considerably larger in relation to the lobule, narrower and more tapering, and with no tendency to break apart.

When only vegetative features are considered there is very close agreement between *R. caloosiensis* and the monoicous *R. complanata*. In fact, there are really no well-defined characters, aside from those relating to the inflorescence, which can be employed to separate these two species when sterile. There is, however, one difference in habit that often can be utilized: *R. complanata* invariably bears flowers even when gemmae are present in abundance; *R. caloosiensis*, on the other hand, rarely fruits, and usually when sterile bears numerous gemmae.

### 3. *Radula Langloisii* sp. nov.

Plants dull green and slightly tinged with yellow: stems 1-2 cm. in length and 0.1 mm. in width, irregularly pinnately and bipinnately branched, the branches wide spreading at first and later converging toward the main axis or bending backward, the growth of the plant frequently continued by a leading branch: stem leaves decidedly imbricate toward the growing tip, less so on older portions of the stem, wide spreading, the keel straight or more rarely only slightly arched; the dorsal lobe  $0.75 \times 0.6$  mm., broadly ovate, the apex rounded, the base free about one-half its length, the free portion auriculate and on younger portions of the plant arching across and some distance beyond the stem, the line of attachment curved; ventral lobe  $0.25 \times 0.25$  mm., subquadrate, appressed to the lobe, the outer free margin and the anterior free margin slightly incurved, the apex slightly prolonged into a blunt tip, the base free about one-

<sup>10</sup> Stephani, F., Sp. Hep. 4: 216. 1910.

fourth its length, the free portion arching a little over the stem, auriculate, the line of attachment nearly straight; rhizoids usually present on the lower portion of the lobule; leaves of the more vigorous branches of the first order essentially like those of the stem, those of the less vigorous branches of the first order and those of the branches of the second order more erect, the lobule larger in proportion to the lobe, more inflated at the base and the keel slightly more arched: cells of the leaf uniformly thin-walled; cells of the leaf margin  $18 \times 18 \mu$ , cells of the median portion of the leaf  $20 \times 18 \mu$ , cells of the basal portion  $23 \times 18 \mu$ : dioicous: male inflorescence intercalary on the stem or a branch, consisting of one to four pairs of subequally bilobed bracts, the bracts decidedly imbricate, much inflated at the base, and the keel strongly arched; dorsal lobe  $0.55 \times 0.25$  mm., erect, broadly rounded at the tip, somewhat constricted above the keel, the base free one-half its length, the free portion extending somewhat across the stem and beyond; the ventral lobe  $0.45 \times 0.2$  mm., erect, rounded at the tip, the base free two-thirds its length, the free portion arching slightly over the stem: female inflorescence terminal on the stem and branches of the first and second orders, with usually a single innovation, the innovation frequently fertile; bracts erect, usually somewhat unequal in size, the lower slightly larger, the keel incurved; the dorsal lobe  $0.85 \times 0.6$  mm., broadly and regularly ovate, the apex broadly rounded; ventral lobe  $0.55 \times 0.45$  mm., somewhat irregular in outline, rounding out abruptly above the keel, the apex blunt: immature perianth  $0.5-0.8$  mm. in length and  $0.8$  mm. in width, strongly flattened, very definitely two-lipped, the cleft shallow on one side and extending usually one-third to one-half the length of the perianth on the other side, the lips very coarsely undulate; the mature perianth about  $1.5$  mm. in length and  $0.75$  mm. in width, somewhat contracted at the mouth, deeply cleft on one side: mature capsules not seen: vegetative propagation by means of occasional discoid gemmae borne on the lobes of the leaves and on the lips of the perianth.

Type collected at Keystone, Louisiana, 1891, *Langlois* (herbarium of C. C. Haynes).

HABITAT AND DISTRIBUTION: growing closely appressed to the bark of trees or mixed with mosses; known only from North Carolina, South Carolina and Louisiana.

NORTH CAROLINA: Jackson Springs, Moore Co., 1905, *C. C. Haynes* (H.).—SOUTH CAROLINA: Summerville, 1889, *C. DuBois* (H.).—LOUISIANA: Coteau, 1890, *Langlois* (H.); Keystone, *Langlois* (H.), TYPE; Bois Lobbé, *Langlois* (H.).

This species somewhat closely resembles *Radula complanata* so far as vegetative features are concerned. In fact, it is difficult

to distinguish between sterile plants of the two species. There are, however, slight differences of a vegetative kind. The leaves of *R. complanata* are always more decidedly imbricate and the lobe does not extend across the stem as far as it does in the other. In fertile material a distinction is a simple matter as *R. Langloisii* is dioicous while *R. complanata* is monoicous. This disposition of sexual organs is a feature that usually can

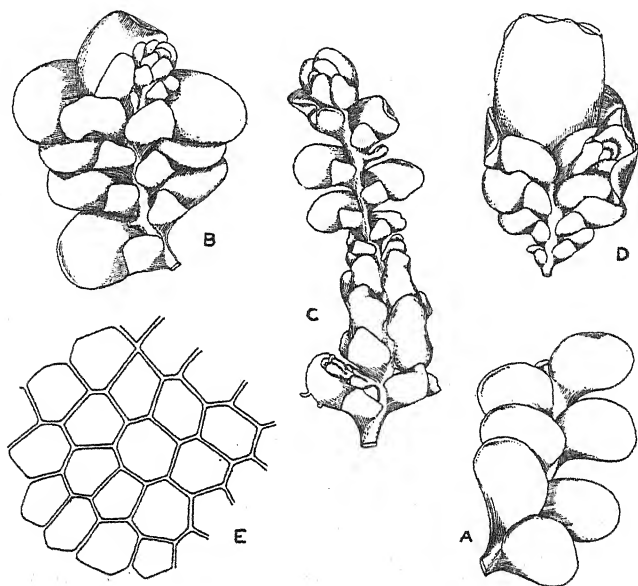


FIG. 9. *RADULA LANGLOISII* Castle. A. Portion of a sterile plant, dorsal view,  $\times 18$ . B. Portion of a female plant showing the female inflorescence with a single sub-floral innovation, ventral view,  $\times 18$ . C. Portion of a male plant showing the intercalary male inflorescence, ventral view,  $\times 18$ . E. Leaf cells,  $\times 450$ .

be employed in separating the two, as *R. complanata* almost always fruits. Moreover, when sterile portions are involved, the abundance of discoid gemmae in *R. complanata* will usually set it apart from the other, in which gemmae are only rarely produced. The female inflorescence suggests that of *R. australis* but differs in that the lobe of the female bract is more broadly ovate and the lobule is larger in proportion to the lobe. The male inflorescence, which is always intercalary on the stem or a

branch, is quite distinct from that of any of our other species. The bracts are few in number, very decidedly imbricate, and become successively smaller from the base of the inflorescence upward. The ventral lobe approaches the dorsal lobe in size. The latter is erect and projects very little to the side. Moreover, there is a pronounced constriction in each bract just above the inflated basal portion. The most striking character possessed by this species is found in connection with the perianth. In all the North American forms this structure is shallowly two-lipped. In *R. Langloisii*, however, the perianth is always deeply cleft on one side.

10. *RADULA ANDICOLA* Stephani, Hedwigia 23: 114. 1884

*Radula viridi-aurea* Spruce, Hep. Amaz. et And. 324. 1885.

*Radula xalapensis* Aust. Hep. Bor.-Am. 88b. 1874. Not Nees & Mont.

*Radula Lescurii* Aust.; Stephani, Sp. Hep. 4: 191. 1910.

Plants usually pale, occasionally dark green in color: stems 1-2.5 cm. in length and 0.15 mm. in width, pinnately but never bipinnately branched, the branches spreading obliquely at an angle of 70-80° and separated by two to four leaves of the stem: stem leaves wide spreading and forming an angle of 80-90° with the stem, usually densely imbricate; the keel slightly incurved and occasionally a little arched in the center; dorsal lobe 1.5 × 1 mm., ovate, arching usually to some extent across and beyond the stem, its base free about one-third the distance, the free portion forming a pronounced auricle, the line of attachment slightly oblique or curved; ventral lobe 0.85-0.7 mm., quadrate, its outer margin parallel to the axis, apex subacute, anterior margin nearly horizontal and usually with a fold, the base free one-half its length, the free portion auriculate and arching nearly across the stem, the line of attachment straight, usually with a small, somewhat pointed swelling bearing rhizoids: leaf cells thin-walled throughout; cells of the leaf margin 18 × 15 μ, median cells 18 × 15 μ, basal cells 25 × 20 μ: male and female inflorescences not known: vegetative propagation by means of discoid gemmae abundant on the margins of the dorsal lobe.

TYPE LOCALITY: America tropica, Ecuador, leg. Krause (Herb. Jack); Silla de Caracas, leg. Birschall (Herb. Kew); Rio Janeiro, leg. Jan Deventer (Herb. Sande-Lacoste).

HABITAT AND DISTRIBUTION: in depressed, dense mats on moist rocks; throughout tropical America, north to District of Columbia and south to Rio de Janeiro.

DISTRICT OF COLUMBIA: Rock Creek Park, 1890, *Waite H44* (H.). This specimen is not typical since the majority of the lobules extend only part way across the stem. An occasional lobule, however, approaches the characteristic form.—WEST VIRGINIA: Beaver Spring, 1892, *Millsbaugh 1551*; Huntington,

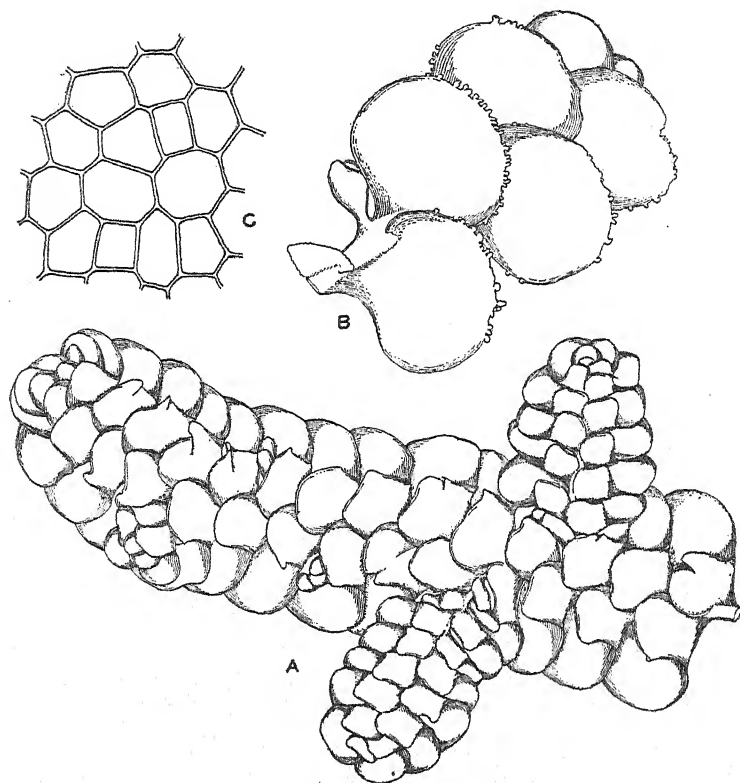


FIG. 10. *RADULA ANDICOLA* Steph. A. Terminal portion of a sterile plant, ventral view,  $\times 18$ . B. Dorsal view of the same,  $\times 18$ . C. Leaf cells,  $\times 450$ .

*Plymale 29*. Both these specimens, like the preceding, possess lobules which in the majority of cases are not typical. Many, however, are sufficiently characteristic to justify including the forms under this species.—NORTH CAROLINA: Woodfin Falls, near Balsam, 1919, *Andrews 278* (*Bryologist* 24: 53. 1921); Moore Spring, Hoke Co., *Schallert 42* (H.).—GEORGIA: Tallulah



Falls, 1874, *Austin*, Hep. Bor.-Am. 88b (distributed as *R. xalapensis* Mont.); Grand Chasm and Glen Ella Spring, vicinity of Tallulah Falls, *Seymour*; Toccoa Falls, *Underwood & Cook*, Hep. Amer. 104 (distributed as *R. xalapensis* Mont.).—CUBA: Monte Verde, *Wright*.—PERU: San Miguel, 1911, *Foote* 44 (Evans, A. W. Trans. Conn. Acad. 18: 313. 1914).

The sterile but gemmiparous specimens from Tallulah Falls have been the source of much confusion. Those collected by Sullivant and Lesquereux were referred by Austin to *R. xalapensis* apparently on the basis of the description by Gottsche in his *Mexikanske Levermosser*. When these specimens were studied by Lindberg he was unable to find any distinction between them and the rare *R. voluta* Taylor of the British Isles.<sup>11</sup> He, therefore, included the latter species under *R. xalapensis* as a synonym and cited also Lindig's material from Colombia, which Gottsche had already referred to *R. xalapensis*.<sup>12</sup> Many years later Stephani took up for the specimens distributed by Austin the name *R. Lescurii* Austin, giving as the place of publication the sixth volume of the Bulletin of the Torrey Botanical Club. No such name appears in this volume so that the species was really a manuscript species of Austin which was first published by Stephani. He had previously referred to *R. Lescurii*<sup>13</sup> without describing it, but at that time regarded it as a synonym of *R. mollis* Lindenberg & Gottsche.

Meanwhile, Stephani had described under the name *R. andicola* a series of specimens without sexual organs from tropical America. According to the description these are apparently identical with the Tallulah Falls specimens, although Stephani made no mention of the characteristic gemmae which are usually so abundantly present. The following year Spruce published his *R. viridi-aurea* based on material from the mountains of Ecuador. This also was described from sterile specimens and again no mention was made of gemmae. In his *Species Hepaticarum* Stephani included *R. viridi-aurea* as a synonym of *R. Lescurii* and extended the range of this species to Bolivia on the south and Costa Rica on the north. In citing material from Peru,

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<sup>11</sup> Acta Soc. Sci. Fenn. 10: 401. 1875.

<sup>12</sup> Ann. Sci. Nat. Bot. V. 1: 143. 1864.

<sup>13</sup> Hedwigia 23: 157. 1884.

Evans noted for the first time discoid gemmae in this species and compared them with those of *R. complanata*.<sup>14</sup>

Unfortunately it has been impossible to obtain for examination the type specimens of *R. andicola* and *R. viridi-aurea*. However, in view of the wide range which Stephani assigns to this species and the close agreement between the Peruvian specimens and those from Tallulah Falls it seems justifiable to include *R. Lescurii* among the synonyms of *R. andicola*.

*R. andicola*, although distinct as a species, stands in close relationship to several other species such as *R. voluta* and *R. mollis*. When compared with *R. voluta* the two are found to differ widely in respect to the lobule, which extends to a much greater distance across and beyond the stem in *R. voluta*. The keel in *R. andicola*, moreover, is almost invariably slightly incurved while in *R. voluta* it is often straight or slightly arched. *R. andicola*, furthermore, usually bears abundantly discoid gemmae, while in *R. voluta*, gemmae are but rarely present.

Stephani, in his original synopsis of the genus,<sup>15</sup> suggests that *R. mollis* Lindenberg & Gottsche and *R. Lescurii* Austin are synonyms. Again comparison of the two reveals marked differences. The lobules of *R. mollis* are still larger and extend even farther across the stem, the free basal portion is usually angular rather than broadly rounded, the leaves are more densely imbricate and gemmae are few in number.

Without doubt *R. andicola*, *R. voluta* and *R. mollis* are members of a group of more or less closely related species. A fourth member of this group is *R. ramulina* Taylor. Here also the most striking difference exists in relation to the lobule which extends to a greater distance across and beyond the stem. Moreover, this species is huge when compared to *R. andicola* and up to the present time is not known to produce gemmae.

II. *RADULA FLACCIDA* Lindenberg & Gottsche; G. L. N.  
Syn. Hep. 726. 1847

*Radula epiphylla* Mitt.; Stephani, Hedwigia 23: 113. 1884.  
*Stephanina flaccida* O. Kuntze, Rev. Gen. Pl. 839. 1891.

Plants dull green: stems 0.5-1.5 cm. in length and 0.06 mm. in width, rather indefinitely pinnately and rarely bipinnately

<sup>14</sup> Trans. Connecticut Acad. Arts & Sci. 18: 313. 1914.

<sup>15</sup> Hedwigia 23: 157. 1884.

branched, the branches 2-5 mm. in length and 0.05 mm. in width, spreading from the stem at an angle of 50-60° and separated by two to five leaves: stem leaves subimbricate, spreading at an angle of 60-70°, usually only slightly falcate, the keel straight or slightly arched; dorsal lobe  $0.9 \times 0.7$  mm., ovate or somewhat obovate, flat, the apex broadly rounded, the base free about one-third its length, the free portion auriculate and arching entirely across the stem but seldom beyond, the line of attachment straight; ventral lobe  $0.3 \times 0.2$  mm., the apex extended into a long, blunt-tipped, frequently curved apex, the base fused to the stem almost its entire length, the line of attachment straight, rhizoids numerous on a pronounced mammilliform swelling; leaves of the axis of the first order essentially like those of the stem; dorsal lobe  $0.6 \times 0.5$  mm.; ventral lobe  $0.13 \times 0.16$  mm., with rhizoids: leaf cells comparatively thin-walled and without trigones; marginal cells  $16 \times 12 \mu$ , median cells  $23 \times 15 \mu$ , and basal cells  $23 \times 15 \mu$ : dioicous: male inflorescence a long, slender, ament, slightly tapering toward the apex, terminal on the stem or branch of the first order; the bracts in three to fifteen pairs, imbricate, much inflated toward the base, the lobes subequal, the keel strongly arched; dorsal lobe  $0.4 \times 0.15$  mm., erect, rounded at the tip; ventral lobe  $0.3 \times 0.15$  mm., obtusely angled at the tip, without rhizoids: female inflorescence terminal on the stem, innovating on both sides, the innovations wide spreading, short and sterile or frequently more elongate and fertile; bracts smaller than the leaves; the keel somewhat inwardly curved; dorsal lobe  $0.55 \times 0.35$  mm., rounded at the apex; ventral lobe  $0.35 \times 0.15$  mm., without an elongate tip, rhizoids absent: perianth 1-1.5 mm. in length, in outline trumpet-shaped with a slightly flaring mouth, terete at the base and strongly flattened above, the mouth shallowly two-lipped, the lips coarsely and irregularly but faintly crenate; the outer layer of the capsule composed of regular more or less isodiametric cells as in *R. complanata*, the vertical radial walls and frequently the horizontal walls strengthened by continuous, more or less regular additional layers of wall material, the tangential walls without thickenings; the inner layer composed of large, thin-walled cells, with the radial walls frequently thickened by uniform thin layers, no thickenings visible on the tangential walls: vegetative reproduction by means of circular, discoid gemmae, borne dorsally in small numbers on the upper margins of the dorsal lobes, one cell in thickness, at maturity 0.5-0.8 mm. in diameter, with several, three to eight, usually five, large cells on the margin representing initial cells, constricted below into a funnel-like structure at the base of which six to eight elongate cells remain attached.

TYPE LOCALITY: in terris Mexicanis prope Hacienda de Fovo foliis *Psychotriae* cuiusdam arctissime irrepens (Liebman).

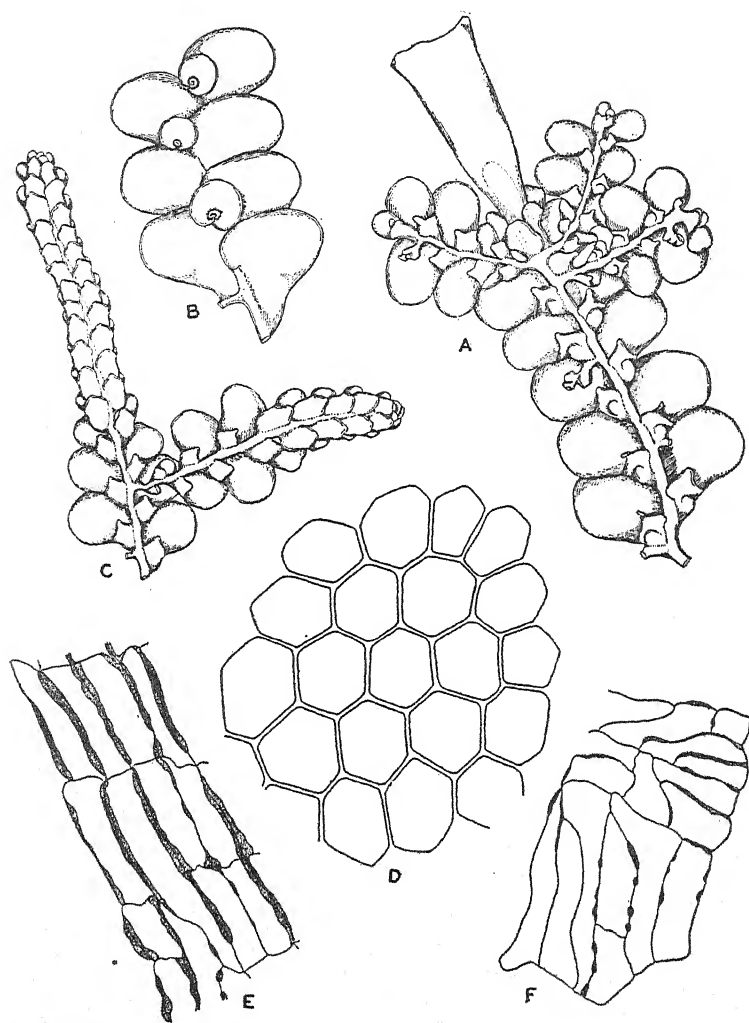


FIG. 11. *RADULA FLACCIDA* Lindenb. & Gottsche. A. Portion of a female plant showing the terminal inflorescence with mature perianth and two sub-floral innovations, ventral view,  $\times 18$ . B. Portion of a sterile plant showing the large, discoid gemmae on the margins of the dorsal lobes, dorsal view,  $\times 18$ . C. Portion of a male plant showing the terminal, amentiform, male inflorescence, ventral view,  $\times 18$ . D. Leaf cells,  $\times 450$ . E. Outer layer of the capsule wall,  $\times 450$ . F. Inner layer of the capsule wall,  $\times 450$ .

HABITAT AND DISTRIBUTION: scattered or in depressed mats, closely appressed to the upper surface of living leaves of trees, shrubs and herbs; throughout the lowlands of tropical America extending as far north as Dade County, Florida; also in tropical West Africa.

FLORIDA: Hattie Bauer Hammock, Dade County, 1915, *Small & Mosier* (Evans, *Bryologist* 20: 24. 1917).—GUATEMALA: vicinity of Secanquim, Alta Verapaz, 1905, *Maxon & Hay* 3211.—CUBA: Monte Toro, *Wright* (distributed in *Hep. Cubenses*).—JAMAICA: Bath, 1903, *Evans* 332; Green River Valley, *Evans* 212.—PORTO RICO: vicinity of Cayey, 1900, *Evans*; vicinity of Utuado, *Wheeler* 992; Mayaguez, *Heller*; Jagua, *Whetsel*.—TRINIDAD: Maraval Valley, Port of Spain, 1913, *Thaxter*; vicinity of Arima, 1920, *E. G. Britton et al.* 641.—BRAZIL: Rio Negro, *Spruce* (distributed in *Hepaticae Spruceanae*).—AFRICA: Niger River, Nigeria, *Barter* (type of *R. epiphylla* from the Mitten herbarium); Cameroons, *Dusen* 427 (distributed as *R. epiphylla* in *Hepaticae Africanae*).

After a careful comparison of the type specimen of *R. epiphylla* Mitten with a number of specimens of *R. flaccida* Lindenberg & Gottsche, there is little doubt that they are one and the same. *Stephani* (*loc. cit.*) gives a brief description of *R. epiphylla* and, at the same time, admits that this species stands very close to *R. flaccida*, the only difference being that the lobules of the former lack the elongate, blunt tip which is so characteristic of *R. flaccida*. As a matter of fact the lobules of the type material from the herbarium of Mitten agree exactly with those of *R. flaccida* collected in tropical America and any slight variation that does exist is no greater than can be found in a single plant of *R. flaccida*. Accordingly, since this species was first described in 1847 under the name *R. flaccida*, it becomes necessary to reduce the later proposed *R. epiphylla* of Mitten to synonymy.

Aside from the extraordinary and almost constant epiphyllous habit of *R. flaccida*, this species is characterized by the production of remarkable bodies for vegetative reproduction. These structures are large discoid gemmae, which arise from the margins of the lobes on the dorsal side of the plant. Miss Ruth Williston has very ably described these gemmae and their development in a paper entitled "Discoid gemmae in *Radula*."<sup>16</sup>

<sup>16</sup> Bull. Torrey Club 39: 329-339. f. 1-37. 1912.

Almost coincident with this account appeared a similar description by Goebel<sup>17</sup> based on African material bearing the name *R. epiphylla* Mitten.

The epiphyllous habit is, apparently, not common among the species of *Radula*. *R. flaccida* is the only one of the species of this genus found within the United States which grows uniformly upon living leaves. There are, however, several other epiphyllous *Radulae* outside the range of this work: *R. Grevilleana* Taylor and *R. sienocalyx* Mont. throughout tropical America and *R. mammosa* Spruce reported only from Bolivia. It is quite possible that one or more of these may extend to tropical Florida as in the case of *R. flaccida*.

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<sup>17</sup> Flora 104: 156. 1912.



## Studies on the flora of northern South America—VIII\*

H. A. GLEASON

### ADDITIONAL NEW SPECIES OF MELASTOMATACEAE

*Miconia subalpina* n. sp. Arborescent; stems above obtusely 4-angled, prominently 4-sulcate, densely villous or subtomentose with spreading or somewhat reflexed simple hairs about 1 mm. long; petioles slender, 3.5-6 cm. long, pubescent like the stem, the hairs frequently stout and flattened; leaf-blades membranous, ovate, 12 cm. long, 8-9 cm. wide, acute, irregularly serrulate, ciliate, broadly rounded at base, upper surface plane, dark green, sparsely pilose in the vein-areas with slender yellowish hairs 0.5-1 mm. long, lower surface pale green, minutely punctulate, pilose along the veins and veinlets with slender, somewhat crooked, whitish hairs mostly 0.5-0.7 mm. long, 7-plexi-nerved; the veins and veinlets obscure above, prominulous beneath; panicles small, few-flowered, 10 cm. long, including the peduncle, densely pubescent like the stem; pedicels 3-5 mm. long; flowers 5-merous; hypanthium broadly campanulate, 6 mm. in length and diameter, densely hirsute with spreading or somewhat reflexed hairs about 1.2 mm. long; calyx-tube prolonged 1 mm. beyond the staminal torus, hirsute like the hypanthium; sepals broadly triangular, 4.5 mm. wide, 1.8 mm. long, subacute, the free margin scarious, glabrous, and densely ciliate with stout hairs 0.5-0.7 mm. long, exterior teeth stout, appressed, about equaling the sepals, 1.5 mm. long, 0.5 mm. thick, hirsute like the hypanthium; petals white, recurved, broadly obovate, 8 mm. wide, 6.5 mm. long, from a truncate base 2 mm. wide, broadly rounded and somewhat retuse at the apex, many-nerved; anthers stout and thick, 3 mm. long, 1.7 mm. thick (radially), 1.2 mm. wide (tangentially), blunt, opening by a single terminal pore 0.4 mm. wide, the connective much thickened below and minutely saccate at base; filaments flat, 3.7 mm. long, 1.7 mm. wide at base, tapering gradually to 0.8 mm. wide at the summit, glabrous; ovary concave at the summit, glabrous; style straight, 9 mm. long, 0.7 mm. in diameter, glabrous; stigma broadly capitate or subpeltate, 0.7 mm. long, 1.7 mm. in diameter.

Type, *Pennell 10,504*, collected in mossy forest, Cerro Tatama, Dept. Caldas, Colombia, alt. 3200-3400 m., 8-10 Sept. 1922, and deposited in the herbarium of the New York Botanical Garden. But few species of the section *Amblyarrhena* have such large flowers, and they mostly have glandular styles and

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\* Contributions from the New York Botanical Garden, no. 277.



filaments. In some superficial characters of foliage it resembles *M. psychrophila*, but I know of no species to which it appears definitely related. Under the arrangement of species in Cogniaux's monograph, it falls in the group 362 to 381.

*Miconia aggregata* n. sp. Arborescent; stems obscurely 4-angled, densely pilose or subtomentose with brown, spreading or somewhat reflexed hairs 1.5 mm. long; petioles stout, 25-35 mm. long, pilose like the stem; leaf-blades firm, ovate, 15-20 cm. long, 8-10.5 cm. wide, obliquely long-acuminate, finely serrulate, broadly rounded at base, upper surface dull green, densely strigose with brown, curved-ascending hairs 1 mm. long, lower surface cinereous, softly subtomentose with spreading, somewhat crooked hairs 1-1.5 mm. long, 5-plexi-nerved, the veinlets 3-5 mm. apart; panicles pyramidal, 9 cm. long, the rachis and branches pubescent like the stem; bracts subulate, 2 mm. long; flowers 5-merous, sessile, in dense, globose, terminal glomerules; hypanthium cylindric, 3.7 mm. long, densely pilose with spreading hairs 1 mm. long; sepals membranous, broadly triangular, 0.4-0.5 mm. long, the free portion glabrous, exterior teeth broadly conic, 0.2 mm. long; petals depressed-ovate, 1.2 mm. long, 1.7 mm. wide; filaments stout, flat, 2.2 mm. long; anthers oblong-elliptic, 1.5 mm. long, obtuse, thicker than wide, unappendaged, opening by a minute terminal pore; ovary glabrous at the summit; style straight, terete, 3.3 mm. long, hirtellous; stigma peltate, 1 mm. in diameter.

Type, *Rusby & Pennell 813*, collected in the forest at "Balsillas," on Rio Balsillas, Dept. Huila, Colombia, alt. 2100-2200 m., 3-5 Aug. 1917, and deposited in the herbarium of the New York Botanical Garden. The species is closely related to *M. capitellata* Cogn., in which the leaves are merely obtuse at base, the pubescence throughout much shorter, the hypanthium smaller, the ovary setulose at the apex, and the style glandular-hirtellous.

*Miconia Pennellii* n. sp. Fruticose or arborescent; stems somewhat flattened or obscurely 4-angled, roughly strigose with short brown hairs; petioles stout, strigose like the stem, 3-4 cm. long; leaf-blades membranous, narrowly ovate to ovate-oblong, 13-18 cm. long, 7-9 cm. wide, acuminate, conspicuously serrulate, rounded at base, upper surface dull green, scabrously strigose with short hairs from a conic base, lower surface ferruginous, foveolate, roughly pubescent with short, crisped or crooked hairs, particularly on the veins, 7-nerved, the outer pair obscure, veinlets 4-5 mm. apart, the tertiary veinlets prominulous beneath; panicles small, congested, 10-15 cm. long, the rachis

and branches densely strigose-hispid; bractlets minute, oblong, acuminate, ciliate; flowers sessile, 5-merous; hypanthium campanulate-cylindric, 4 mm. long, densely strigose with stout, ascending hairs about 0.5 mm. long; sepals membranous, broadly triangular-ovate, 1.5 mm. long, rounded at the apex, the exterior teeth stout, conic, 1 mm. long, spreading or somewhat recurved, strigose like the hypanthium; petals broadly obovate, 2.7 mm. long, glabrous; filaments stout, flat, 2.5 mm. long, 0.8 mm. wide, minutely and sparsely hirtellous; anthers stout, oblong, 1.6 mm. long, opening by a small terminal pore, unappendaged; ovary setulose at the tip; style stout, 3.3 mm. long, 0.8 mm. in diameter, tapering slightly upward, hirtellous, not glandular; stigma peltate, 1 mm. in diameter.

Type, *Killip 7951*, collected in the forest at "La Gallera," Micay Valley, Dept. El Cauca, Colombia, alt. 2000-2200 m., 1 July 1922, and deposited in the herbarium of the New York Botanical Garden. The type is in flower; the fruiting condition is represented by *Pennell 7577*, from "San Jose," San Antonio, Dept. El Cauca, 2400-2700 m., 1 July 1922. Of the section *Amblyarrhena*, it resembles *M. capitellata* in habit, but in that species the leaves are 7-plexi-nerved and the pubescence of the stem is spreading. *Lehmann 5921* and *8519* are conspecific.

*Miconia penicillata* n. sp. Shrubby, 5 dm. tall; stems nearly terete, persistently and densely stellate-tomentose and sparsely pilose with spreading hairs 1.5 mm. long, bearing a tuft of slender apical branches; petioles slender, 2-3 cm. long, pubescent like the stem; leaf-blades firm, ovate-oblong, 8-10 cm. long, 4-5 cm. wide, sharply and abruptly acuminate, finely serrulate, broadly acute at base, upper surface dark green, bullate-strigose with short stiff hairs, lower surface ferruginous, foveolate, thinly but closely stellate-tomentose and sparsely pilose on the principal veins, 7-plexi-nerved, the veinlets prominently elevated beneath; panicle widely spreading, freely branched, on a long peduncle, the rhachis and branches pubescent like the stem; bracts obovate, 2-3 mm. long, stellate-tomentose; flowers 5-merous, sessile, crowded in dense terminal and subterminal glomerules; hypanthium obconic, 3 mm. long, densely brown stellate-tomentose; sepals broadly ovate, 0.6 mm. long, 1.1 mm. wide, the margin scarious, the exterior teeth minute, conic; petals white, elliptic-obovate, 2.3 mm. long, 1.6 mm. wide, glabrous, entire; filaments 2.6 mm. long, glabrous, the lower three-fourths flat, 0.4 mm. wide, the upper one-fourth slender; anthers oblong, blunt, thick, 1.4 mm. long, broadest (0.6 mm.) near the apex, opening by a small terminal pore, the connective thick, not prolonged or appendaged; ovary glabrous at the

summit; style straight, terete, 3.3 mm. long, gradually thickened upward, glabrous; stigma capitate, 0.8 mm. in diameter.

Type, *Pennell & Killip 5808*, collected in forest, on a peak southeast of La Cumbre, Dept. El Valle, Colombia, alt. 2150–2400 m., 14–19 May 1922, and deposited in the herbarium of the New York Botanical Garden. The species is a member of the section *Amblyarrhena* and related to *M. capitellata* Cogn. It differs from that and allied species in the conspicuous stellate tomentum on the stem, lower leaf-surface, inflorescence, and hypanthium, coupled with the prominent, long, penicillate hairs on the stem and panicle.

*Miconia minuta* n. sp. Fruticose; stems obscurely 4-angled and lightly 4-sulcate, sparsely stellate-furfuraceous, glabrescent with age; petioles slender, 2 cm. long, channeled above, minutely furfuraceous; leaf-blades membranous, oblong-elliptic, 18 cm. long, 7–8 cm. wide, sharply acuminate, entire, conspicuously but finely ciliate (about 16 cilia per cm. of margin, 0.5 mm. long), cuneate at base, dark green and glabrous above, or sparsely furfuraceous along the midvein, pale green, glabrous on the surface, and minutely and sparsely furfuraceous on the veins beneath, 7-nerved, the outer pair of veins 0.5 mm. from the margin, the next pair 2 mm. from the margin, veinlets strongly ascending, 3–4 mm. apart; panicle freely branched, 11 cm. long, the rhachis and branches conspicuously stellate-furfuraceous and also pilose with spreading hairs 0.7 mm. long; pedicels glabrous, 0.5 mm. long; flowers 5-merous; hypanthium broadly campanulate, 1.2 mm. long by 1.3 mm. wide, glabrous; sepals depressed-triangular, 0.2 mm. long, 0.5 mm. wide, subacute, glabrous, the exterior teeth triangular, acute, less than 0.1 mm. long; petals oblong-obovate, white, 0.8 mm. long, 0.5 mm. wide, rounded at the apex; filaments 1 mm. long, glabrous, the lower three-fifths stout, the upper two-fifths slender; anthers oblong, 0.6 mm. long, broadest near the summit, 0.2 mm. wide, somewhat attenuate at base, the anther-sacs minutely gibbous at the base anteriorly, opening by two wide terminal pores; ovary rounded at the summit, glabrous, radially ribbed; style straight, stout, terete, 0.7 mm. long, 0.2 mm. in diameter; stigma capitate, 0.3 mm. in diameter.

Type, *Rusby & Pennell 791*, collected in forest at "Balsillas," on the Rio Balsillas, Dept. Huila, Colombia, alt. 2100–2200 m., 3–5 Aug. 1917, and deposited in the herbarium of the New York Botanical Garden. It finds its nearest relative apparently in *M. Lehmannii* Cogn., from which it differs in its ciliate leaves, its pilose inflorescence, and its short style. Its flowers are smaller than those of any other species of *Miconia* known to me.

**Miconia mimica** n. sp. Arborescent; stems prominently 4-sulcate with rounded ribs, glabrous, or furfuraceous-annulate at the nodes above; petioles stout, 25-40 mm. long, glabrous below, conspicuously furfuraceous on the upper side at the summit; leaf-blades thin and membranous, elliptic-obovate, the members of each pair somewhat unequal, 12-17 cm. long, 6-8.5 cm. wide, abruptly and sharply acuminate, minutely denticulate with ascending or appressed teeth (about 8 teeth per cm. of margin, 0.3 mm. long), obtuse to subrotund at base, dark green and glabrous above, pale green and glabrous beneath, 5-nerved, the outer pair obscure and submarginal, the middle three lightly impressed above, prominent beneath, veinlets conspicuous, especially beneath, tertiary veinlets conspicuously reticulate; panicle freely branched, spreading, 12 cm. long, glabrous or sparsely furfuraceous at the nodes; bractlets none or caducous; pedicels 0.3-0.8 mm. long; flowers 5-merous; hypanthium sub-urceolate, 1.4 mm. long, 1.3 mm. in diameter, brown, glabrous; sepals broadly rounded, 0.7 mm. wide, 0.2 mm. long, glabrous, the free margin scarious, exterior teeth broadly triangular, appressed, obtuse, less than 0.1 mm. long; petals broadly obovate, pale yellow, 0.8 mm. long, 0.7 mm. wide, glabrous; filaments glabrous, 1 mm. long, the lower three-fifths stout, the upper two-fifths slender; anthers oblong-obovate, 0.8 mm. long, the anther-sacs 0.5 mm. long, 0.3 mm. wide, opening by a double terminal pore of the same width, connective thickened on the back and prolonged 0.3 mm. below the anther-sacs, minutely bigibbous anteriorly; ovary rounded at the summit, glabrous, strongly radially ribbed; style straight, terete, glabrous, 2 mm. long, 0.3 mm. in diameter; stigma peltate, 0.6 mm. in diameter.

Type, *Killip 7936*, collected in forest at "La Gallera," Micay Valley, Dept. El Cauca, Colombia, alt. 1900-2000 m., 1 July 1922, and deposited in the herbarium of the New York Botanical Garden. It is a member of the section *Cremanium*, and bears a strong resemblance to *M. minuta* Gleason in its general appearance and small flowers. It differs in its non-ciliate leaves, its nearly glabrous inflorescence, its broader exterior calyx-teeth, its longer style and the conspicuously prolonged connective. It also closely resembles *M. coelestis* (Pav.) Naud., a plant of Peru and Bolivia with sessile flowers.

**Miconia cuneifolia** n. sp. Low tree; stems obtusely 4-angled and densely and closely ferruginous-tomentulose when young, becoming terete and glabrous with age; petioles slender, 12-15 mm. long, nearly terete, thinly tomentulose; leaf-blades firm, oblong-obovate, 7-10 cm. long, 22-35 mm. wide, sharply acuminate, entire, slightly revolute, cuneate from above the

middle to the base, upper surface dark green, slightly rugose, glabrous, lower surface closely ferruginous-tomentose with stellate hairs, 5-nerved, the veinlets 1.5-2 mm. apart; panicles 8 cm. long, the rhachis and branches densely ferruginous-tomentose; flowers 6-merous, sessile, closely crowded in terminal and subterminal glomerules; hypanthium campanulate, 2.3 mm. long, densely but closely stellate-tomentulose; sepals broadly triangular, 0.4 mm. long, subacute, pubescent like the hypanthium, the exterior teeth apparently none; petals rotund-spatulate, 1.5 mm. long, 1.1 mm. wide, glabrous; anthers obovate-oblong, 1.7 mm. long, 0.7 mm. wide, opening by two broad terminal pores, somewhat attenuate to the base and minutely 2-gibbous, connective thickened below and minutely saccate at the base posteriorly; filaments 3-4 mm. long, glabrous, bent at three-fourths of their length, the basal portion stout, somewhat flattened, 0.3 mm. wide, the distal portion slender; ovary broadly ovoid-conic at the summit, glabrous, radially ribbed; style straight, 3.3-4 mm. long, terete, glabrous; stigma capitate, 0.6 mm. in diameter.

Type, *Rusby & Pennell 831*, collected at edge of a bog, "Balsillas," on the Rio Balsillas, Dept. Huila, Colombia, alt. 2100-2200 m., 3-5 Aug. 1917, and deposited in the herbarium of the New York Botanical Garden. It is a member of the section *Cremanium* and related to species 429-431 of Cogniaux's monograph, but differing from any of them in the long, cuneate leaf-base.

*Miconia turgida* n. sp. Arborescent; stems stout, 4-angled, lightly 4-sulcate, and thinly furfuraceous above, becoming terete and glabrous in age; petioles stout, 4-5 cm. long, channeled above, flattened toward the summit, thinly furfuraceous; leaf-blades thick, elliptic, 23 cm. long, 10.5 cm. wide, abruptly acuminate to a short obtuse apex, remotely spinulose-denticulate (2-3 teeth per cm. of margin, 0.4 mm. long), acute at base, yellow-green and glabrous above, with deeply impressed veins, brownish-green, minutely punctate on the surface, and sparsely furfuraceous on the veins beneath, 5-nerved, the veins prominent beneath, the outer pair submarginal, the veinlets ascending, 3-4 mm. apart, the tertiary veinlets reticulate; panicle sessile, 10 cm. long, the rhachis and branches 4-angled, thinly furfuraceous, especially at the nodes; flowers 5-merous, on pedicels 1 mm. long; hypanthium campanulate, 2.7 mm. long, 3.1 mm. in diameter, glabrous, minutely punctate; sepals broadly ovate, 0.6-0.8 mm. long, glabrous, truncate or rounded, the margin membranous, exterior teeth flattened, conic, appressed, 0.5 mm. long, blunt, minutely puberulent; petals broadly obcordate from a truncate base, 1.7 mm. long and wide, white,

glabrous; filaments 2.7 mm. long, 0.6 mm. wide at base, gradually narrowed to 0.3 mm. at the summit, the lower three-fifths strongly turgid; anthers obovate, 1.9 mm. long, 0.9 mm. wide, the two terminal pores together 0.5 mm. wide, attenuate and bigibbous at base, the connective strongly thickened and prolonged posteriorly into a blunt appendage 0.3 mm. long; ovary hemispheric at the summit, glabrous, with 10 rounded radial ribs not elevated around the style; style straight, terete, 3.3 mm. long, 0.4 mm. in diameter, glabrous; stigma capitate, 0.8 mm. in diameter. FIG. 1.

Type, *Pennell 9302*, collected in forest at "Pinares," above Salento, Dept. Caldas, Colombia, alt. 2600-2800 m., 2-10 Aug. 1922, and deposited in the herbarium of the New York Botanical Garden. The type specimen exhibits a pair of leaves of the dimensions indicated on the old wood near the base, and a young flowering branch from the base of a fruiting panicle.

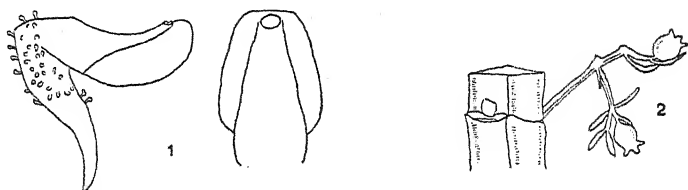


FIG. 1. *MICONIA TURGIDA* Gleason, stamens  $\times 7.5$ .

FIG. 2. *KILLIPIA QUADRANGULARIS* Gleason, portion of inflorescence, natural size.

On the latter the leaves are smaller, and the members of each pair unequal in size, varying from 65 by 23 mm. to 90 by 40 mm. for the smaller, and from 120 by 48 mm. to 150 by 62 mm. for the larger, the smaller pairs being the uppermost. In these the petioles range from 10 to 16 mm. long. The fruit is globose, 6 mm. in diameter. The plant bears a superficial resemblance to *M. scutata* Gleason, but belongs to the section *Chaenopleura*. Under the artificial disposition of the species in Cogniaux's monograph, it stands near species 494 to 498, and differs from them in the leaves acute at base and in numerous details of structure.

***Miconia Cladonia* n. sp.** Tall shrub or low tree; stems nearly terete, sparsely furfuraceous when young with freely branched hairs nearly 1 mm. long, glabrescent and verrucose in age; petioles stout, 6-10 mm. long, pubescent like the stem;

leaf-blades broadly elliptic to obovate-oblong, or rarely oblong-ovate, thick and firm, 4.5–7 cm. long, 23–36 mm. wide, abruptly subacuminate, spinulose-denticulate with appressed teeth (4 or 5 teeth per cm. of margin, nearly 1 mm. long), broadly acute at base, dark yellowish-green and glabrous above, pale yellow-green and minutely punctate on the surface beneath and conspicuously tomentose along the veins with freely branched hairs about 0.5 mm. long, 3-nerved, the veins lightly impressed above, elevated beneath, the veinlets obscure above, barely prominulous beneath, the tertiary veinlets invisible; panicles sessile, congested, 4 cm. long, the rhachis and branches 4-angled, pubescent like the stem; pedicels 0.7 mm. long, minutely pubescent, or many flowers sessile; bracts elliptic, 4 mm. long, 1.6 mm. wide, brown, acute, densely ciliate; flowers 5-merous; hypanthium obconic-campanulate, yellowish-green, 2.1 mm. long, minutely punctulate; sepals semicircular, 0.6 mm. long, 1.3 mm. wide, the free margin scarious, somewhat erose-denticulate, exterior teeth triangular, as wide as the sepals, 0.3 mm. long, minutely and acutely apiculate; petals white, obovate-rotund, 2.5 mm. long, 2 mm. wide; filaments 2.6 mm. long, 0.5 mm. wide at the base, gradually attenuate to 0.2 mm. wide at the apex, slightly bent at three-fifths of their length, the lower portion somewhat turgid, the upper nearly terete; anthers 1.2 mm. long, obovate, opening by a triangular notch 0.5 mm. wide by a third as deep, the anther-sacs minutely prolonged at base, connective strongly thickened on the back, prolonged into an ovoid spur 0.2 mm. long at the base posteriorly; ovary glabrous at the summit, ovoid, prominently elevated around the style; style straight, terete, glabrous, 3 mm. long; stigma capitate, 0.7 mm. in diameter.

Type, *Pennell 7544*, collected in the shrub zone ("paramillo") on Mount El Trueno, Dept. El Cauca, Colombia, alt. 2700–3000 m., 29, 30 June 1922, and deposited in the herbarium of the New York Botanical Garden. Other specimens, agreeing with the type in every respect except minor details of dimensions, and all from El Cauca, are *Pennell 7529*, same locality, altitude, and date, *Pennell 7498*, shrub zone on Mount El Derrumbo, alt. 2700–3000 m., 29 June, 1922, and *Pennell & Killip 7434*, bushy forest, "San Jose," San Antonio, alt. 2400–2700 m., 28 June, 1922. The characteristic features of the plant are its yellowish-green foliage and the prominent zones of branched hairs along the veins. Under the lens these hairs resemble the reindeer moss, and have suggested the specific name. It is a member of the section *Chaenopleura*, and closely related to *M. flavescens* Cogn., of Bolivia. In the latter the leaves are rounded

or subcordate at base, somewhat 3-plex-nerved, and closely furfuraceous along the veins; the stem is densely brown-furfuraceous when young, the bracts are none or caducous, and the flowers are on pedicels 1-3 mm. long.

*Clidemia cymosa* n. sp. Stem shrubby, apparently erect, terete, hirsute or subhispid with straight, spreading hairs 1.5-2 mm. long, and also short-pubescent around the nodes; petioles stout, 5 mm. long or less, densely hirsute with spreading hairs 2.5 mm. long and also puberulent; leaf-blades membranous, broadly round-ovate, abruptly acuminate, conspicuously and irregularly dentate (4-6 teeth per cm. of margin, 0.5-2 mm. high), cordate at base, 7-nerved, the larger with an obscure additional pair, upper surface plane, sparsely hirsute with straight hairs 1-1.5 mm. long and also minutely puberulent when young, lower surface hirsute, especially on the veins, with white hairs mostly 0.7 mm. long; cymes axillary, freely branched, lax and open, 20 cm. long, 15 cm. wide, hirsute like the stem, the ultimate branches bearing mostly 2 flowers on pedicels 4-5 mm. long; flowers 4-merous, bracted by several stout setae 3-4 mm. long; hypanthium narrowly obovoid-oblong, 5 mm. long, sparsely setose and closely and minutely tomentulose; sepals membranous, depressed-ovate or nearly semi-circular, 0.7 mm. long, tomentulose, the exterior teeth stout, spreading, conic, 1.3 mm. long, setose, tomentulose; petals apparently white, obovate-oblong, 2.3 mm. long, 1.7 mm. wide, rounded at the apex, glabrous; stamens 8; filaments stout, flattened, 2.4 mm. long, 0.7 mm. wide; anthers linear, 3.5 mm. long, tapering to the apex, unappendaged; ovary truncate, glabrous, 4-locular; style stout, terete, 5.5 mm. long; stigma capitate.

Type, *Pennell 1510*, collected on a moist bank, Villavicencio, Intendencia Meta, Colombia, alt. 500 m., 26-31 Aug. 1917, and deposited in the herbarium of the New York Botanical Garden. The leaves vary in size in each pair. The largest leaf, the opposite of which is missing, measures 20 cm. long by 15.5 cm. wide; a second pair measures 19 by 11.5 and 12 by 7.5, and another set is 10 by 6 and 7 by 5 cm. The collector noted that the fruit was fleshy and purple. *C. cymosa* is most closely related to *C. impetiolearis* Cogn. and *C. ciliata* D. Don, notwithstanding the fact that a difference in the number of leaf-nerves led Cogniaux to place these two species a few pages apart in his monograph. Our species is distinguished by the setose or hirsute pubescence, the almost entire absence of stellate pubescence, the larger leaves and cymes, and the shorter external teeth of the calyx.



**Killipia** n. gen.

Flowers 5-merous, pedicelled, in axillary bracted cymes fascicled in the axils; hypanthium broadly campanulate; sepals erect, with small exterior teeth; petals yellow, broadly ovate, obtuse, incurved at the summit; stamens all alike; anthers oblong, truncate, opening by a large terminal pore, minutely tuberculate at base; connective slender, not prolonged at base, with two minute, ovoid, saccate appendages on the dorsal side; filaments articulated directly to the anthers, curved, thickened below, tapering to the summit; ovary inferior, its summit depressed conic, glabrous; style straight, stout; stigma punctiform.

**Killipia quadrangularis** n. sp. Arborescent; the branches stout, glabrous, acutely quadrangular or narrowly 4-alate, the internodes 10-15 mm. long when young, lengthening in age to 25 mm.; leaves opposite, the members of each pair essentially equal; leaf-blades stiff, thick, narrowly elliptic-oblong, 9-13 cm. long, 20-28 mm. wide, strongly ascending, acute, subrevolute, minutely setulose-serrulate with appressed teeth (about 3-8 teeth per cm. of margin, 0.1-0.2 mm. long), gradually narrowed below to a short, stout, flat, winged petiole 8-10 mm. long by 2-3 mm. wide, strongly 3-nerved, with an additional obscure intramarginal pair, upper surface dull yellowish-green, glabrous, rugose with strongly impressed veins and lightly impressed, crooked, reticulate veinlets, lower surface red, the strongly elevated veins and reticulate plane veinlets black, glabrous, the petiole and nodes thinly furfuraceous; cymes 3-5 in each axil, about 2 cm. long, 3-flowered, bearing two bracts at the base of the lateral pedicels and two below each flower; bracts red, linear-elliptic, 5-7 mm. long, 0.8-1 mm. wide, narrowed to both ends, sparsely setulose-ciliate; pedicels red, 5 mm. long, jointed at the middle; hypanthium reddish, broadly campanulate, 2.1 mm. in diameter, 1.8 mm. long, obscurely ribbed, glabrous; sepals ovate, 1.6 mm. long, 1.2 mm. wide, broadly rounded or truncate at the apex, glabrous, the exterior teeth stout, closely appressed, triangular, acute, 1 mm. long, 0.6 mm. wide; petals yellow, broadly ovate, 5 mm. long, 3 mm. wide, membranous, rounded at the apex, glabrous; stamens 10; anthers 2-celled, oblong, slightly broadened distally to the truncate apex, 1.2 mm. long, 0.4 mm. wide, minutely tuberculate at base, the appendages of the connective 0.2 mm. long; filaments sigmoid, 1.5 mm. long, 0.4 mm. wide below, tapering to a terete summit 0.15 mm. in diameter; ovary half as long as the hypanthium, its summit obscurely 10-ribbed; style terete, 2.5 mm. long, 0.35 mm. in diameter, glabrous; stigma punctiform; fruit unknown. FIG. 2, page 453.

Type, *Killip 8007*, collected in the forest at "La Gallera,"

Micay Valley, Dept. El Cauca, Colombia, alt. 2200–2600 m., and deposited in the herbarium of the New York Botanical Garden.

Notwithstanding the lack of mature fruit or seeds, *Killipia* is obviously a member of the tribe Miconieae, as shown by the structure of the stamens, the inferior ovary, the presence of exterior calyx-teeth, and the lateral cymules. It is distinguished from *Ossaea*, *Henriettella*, and *Myriaspora* by its obtuse petals; from *Loreya* by its differentiated sepals; from *Henriettea* by its truncate anthers; from *Microphysca* by its wingless hypanthium and absence of formicaria; from *Myrmedone*, by its 5-merous flowers; from *Maieta* by its quadrangular branches; from *Bellucia* by its small flowers and external calyx-teeth; from *Mecranium* by the absence of a prolonged connective; and from *Clidemia* by its stout anthers and glabrous flowers and foliage.

*Ossaea grandifolia* n. sp. Section Octopleura; probably arborescent; branches stout, brown, terete or nearly so, glabrate; leaves firm, oblong-obovate, 30–35 cm. long, 12–15 cm. wide, attenuate at base along the stout petiole almost to its base, entire, rounded at the apex, glabrous above, minutely puberulent along the midvein beneath, distinctly 5-plei-nerved, the lateral veins arising about 25 and 40 mm. from the base, veinlets conspicuous, 6–7 mm. apart; panicles 10 cm. long, densely furfuraceous, the branches spreading; flowers sessile, 4-merous; fruiting hypanthium depressed-globose, strongly 8-ribbed, minutely stellate-puberulent, 2 mm. long.

Type, *Killip 5120*, collected in forest at Cordoba, Dept. El Valle, Colombia, alt. 80–100 m., 6, 8 May 1922, and deposited in the herbarium of the New York Botanical Garden. Although the specimen unfortunately bears no flowers, and notwithstanding the fact the the single panicle appears to be terminal, I have placed this interesting plant in the genus *Ossaea*, because of its strongly ribbed fruit and general resemblance to *O. diversifolia*. It differs from this species in its glabrous foliage and 4-merous flowers.

*Blakea fasciculata* n. sp. Fruticose; flowering axes subterete, minutely and closely furfuraceous, the internodes 10 cm. long; petioles stout, 6 cm. long, finely striate, sparsely and minutely furfuraceous; leaf-blades broadly elliptic to elliptic-obovate, membranous, 15–18 cm. long, 8–10.5 cm. wide, rounded above to a triangular cusp 5 mm. long, minutely denticulate (teeth salient, blunt, 0.2 mm. high, 3 or 4 per cm. of margin), rounded

or barely subcordate at base, 7-nerved, the veinlets somewhat ascending, 2.5-3 mm. apart, glabrous on the surface, minutely furfuraceous on the veins and on the veinlets beneath; flowers 6-merous, in crowded axillary fascicles, on 4-angled, minutely furfuraceous pedicels 1-2 cm. long; bracts 4, separate, closely surrounding the calyx in bud, somewhat surpassing the sepals in anthesis, obovate, obtuse or subacute, narrowed to the base, minutely furfuraceous, obscurely nerved; hypanthium broadly campanulate, 5 mm. long, glabrous, 12-ribbed within between the ovary and the staminal torus; sepals firm or coriaceous, brown, ovate-triangular, 3.5 mm. long and wide, obtuse, glabrous; petals pink, 12 mm. long, minutely ciliolate, otherwise glabrous, longitudinally nerved; stamens all alike, strongly inflexed; anthers connivent, stout and thick, oblong-elliptic, 5 mm. long, 2.5 mm. wide, laterally flattened, rounded at the summit, opening by minute terminal pores; connective thick, not prolonged below the anthers, the posterior spur stout, conic, 1.5 mm. long, wrinkled, apiculate, channeled on the anterior side; filaments flat, 5 mm. long, 1.3 mm. wide, tapering slightly to the summit; ovary inferior, the summit conic around the depressed center, sharply 12-ribbed, each rib ending in a minute erect free lobe; style terete, straight, 12 mm. long; stigma punctiform.

Type, *Pennell 4466*, collected in forest at Antizales, Dept. Bolivar, Colombia, alt. 1200-1600 m., 25, 26 Feb. 1918, and deposited in the herbarium of the New York Botanical Garden. Apparently related to *B. latifolia* (R. & P.) D. Don, but differing in its larger leaves and calyx and in its leaves rounded at base.

*Blakea brachyura* n. sp. Arborescent; branches terete or nearly so, glabrous; petioles stout, 10-15 mm. long, glabrous or verrucose; leaf-blades dull green, thick and firm, broadly elliptic, the largest 77 mm. long by 45 mm. wide, abruptly acuminate into an apical cusp 5-7 mm. long, entire, obtuse at base, 5-nerved, the veinlets obscure, 0.3-0.5 mm. apart, glabrous on both sides, minutely and densely punctate above; flowers 6-merous, solitary or paired in the upper axils, on somewhat verrucose pedicels 20-35 mm. long; bracts 4, broadly rounded, coriaceous, or chartaceous at the margin, glabrous, the outer pair somewhat connate at base, 4 mm. long, the inner pair 5 mm. long; hypanthium coriaceous, broadly campanulate, 6 mm. long, the sepals obsolete; petals white, 9 mm. long, abruptly widened at the middle from a darker base to a membranous acute tip 7 mm. wide; anthers narrowly oblong, 4.5 mm. long, opening by 2 terminal pores, the stout connective prolonged at the base posteriorly into a subulate spur 0.7 mm. long; filaments stout, narrowly elliptic-oblong, 3 mm. long, 0.7 mm. wide.

Type, *Pennell 10,742*, from the edge of the forest at "Buenos Aires," north of Supia, Dept. Caldas, Colombia, alt. 2000-2200 m., 18, 19 Sept. 1922, and deposited in the herbarium of the New York Botanical Garden. It is related to *Blakea rostrata* O. Berg, a Peruvian species with more caudate leaves, shorter pedicels, and more pubescent pedicels and bracts.

**Blakea quadriflora** n. sp. Glabrous throughout; stems woody, subterete, or somewhat flattened below the nodes; petioles 3 cm. long, strongly channeled above; leaf-blades membranous, bright green, broadly elliptic or slightly obovate, 16 cm. long, 10.5 cm. wide, rounded to an abruptly cuneate base, entire, rounded above to a triangular apex 3-5 mm. long, 5-nerved, the nervules mostly 2 mm. apart; flowers 6-merous, in opposite axillary fascicles of 4; pedicels strongly flattened, somewhat broadened upwards, 25-35 mm. long; bracts 4, free, pale green, broadly obovate from a cuneate base, rounded or minutely apiculate at the apex, both outer and inner about 1 cm. long; hypanthium short-cylindric or broadly campanulate, 6 mm. long and the same in diameter; sepals reduced to callous teeth 0.3 mm. long; petals white, broadly rotund, 5.5 mm. long; anthers coherent in a ring, broadly oblong, 3 mm. long, with a minute basal protuberance; filaments as broad as the anthers, 2 mm. long; style narrowly conic, 5 mm. long.

Type, *Hitchcock 21,160*, collected between La Chorita and Portovelo (Gold Mine near Zaruma), Prov. Oro, Ecuador, alt. 1000-2000 m., 28 Aug. 1923, and deposited in the herbarium of the New York Botanical Garden. Related to species 8 to 13 in Cogniaux's monograph, of which only *B. latifolia* (R. & P.) D. Don and *B. podagrica* Triana are glabrous: of these two the former has solitary flowers and the latter long-acuminate bracts.

**Topobea alternifolia** n. sp. Probably arborescent; branches slender, terete or nearly so, the leafy twigs conspicuously zigzag, thinly but closely furfuraceous-tomentulose when young, becoming glabrate with age, the upper internodes about 1 cm. long; leaves alternate; petioles slender, channelled above, minutely furfuraceous on the back, 7-10 mm. long; leaf-blades thin, oblong-elliptic to oblong-obovate, abruptly acuminate into a linear-caudate apex, entire, cuneate at base, glabrous and shining on both sides, 5-plexi-nerved, the veinlets conspicuous, about 1 mm. apart; flowers 6-merous, axillary, solitary, on strongly furfuraceous pedicels 20-25 mm. long; hypanthium globose, furfuraceous, 3 mm. long, much exceeding the 4 minute, broadly rounded, furfuraceous bracts; calyx prolonged about 1 mm. beyond the hypanthium, the sepals triangular, thinly furfuraceous, 1.5 mm. long.

Type, *Killip 5125*, collected in the forest at Cordoba, Dept. El Valle, Colombia, alt. 80-100 m., 6, 8 May 1922, and deposited in the herbarium of the New York Botanical Garden. The leaf-blade is 25-35 mm. wide by 60-90 mm. long, of which 10-20 mm. is included in the conspicuous linear tip. The pedicels arise not only from the axils of the developed leaves, but also opposite them, in the axil of the abortive leaf. *T. alternifolia* is related to the last three species of Cogniaux's monograph, all of which have leaves rounded or cordate at the base and the smaller leaf of each pair present, as well as differing in other details.

## A critical consideration of Hagström's work on *Potamogeton*<sup>1</sup>

HAROLD ST. JOHN

(WITH A TEXT FIGURE)

In the Swedish periodical cited below<sup>2</sup> the late Dr. J. O. Hagström published a monograph of the genus *Potamogeton*. This is by no means the first, for during the last thirty-one years there have been five such general treatments, by Morong, Fryer, Fischer, Ascherson and Graebner, and Taylor.

At least one copy of Hagström's work must have reached the United States soon after its publication in 1916. In the *Botanical Gazette* a short review or notice by J. M. C. [oulter] was printed in 1917.<sup>3</sup> The blockade of the North Sea, however, cut off the importations, and none of the libraries available to the writer in Boston were able to obtain a copy at that time. In 1918 and 1919, when in Paris, the writer renewed efforts to see Hagström's publication, but no copies were available there. Not until 1922 was his attempt to purchase a copy successful. A review of this paper was published in 1919 by the English specialist Arthur Bennett,<sup>4</sup> but it includes almost entirely different material from that presented here.

The object in reviewing Hagström's "Critical Researches" is to point out its resemblances and divergencies from previous monographs, and particularly to scrutinize the treatment of the North American species.

Hagström's studies on *Potamogeton* began in 1891. He made collections in the field, and studied those available in the principal herbaria in Sweden, Norway, and Denmark. He seems to have had all the important literature on the genus available. Judging by the specimens cited, these herbaria contain abundant material from the Scandanavian countries, a moderate amount from England, Germany, and the rest of Europe, and only small

<sup>1</sup> Contribution from the Botany Department, State College of Washington, No. 1.

<sup>2</sup> Hagström, J. O. *Critical Researches on the Potamogetons*. Kungl. Svenska Vetenskapsakademiens Handlingar 55: 1-281. f. 1-119. 1 N 1916.

<sup>3</sup> Bot. Gaz. 64: 87-88. 1917.

<sup>4</sup> Trans. Proc. Bot. Soc. Edinburgh 27: 315-326. 1919.

collections from Africa, Asia, Australia, South America, and North America. The number of specimens from the latter area is small. The portions of this continent represented are principally New England, and to a lesser extent the North Atlantic states, the upper Mississippi valley, and Ontario. The collectors in most cases were Tuckerman, Robbins, Faxon, and Morong. In many cases the data are incomplete, the localities being simply *Nov. Angl.*, or *Nov. Ebor.*

In the introductory portion, Hagström gives a lengthy description of the morphology of the genus. The external morphology is well covered, as has been done by previous authors. The internal morphology of the plant in general, and of the leaf and stem in particular is treated at equal length. He describes the nature of the stem, and particularly as to its epidermal cells, its endodermis, and its stelar arrangement. He tells of the varying types found in this stele at the nodes, internodes, at different internodes on the same stem, and in stranded or floating stems of the same plant. Cross sections of the stem for systematic classification should be cut, he says, "at about the middle of the spike-bearing shoot."<sup>5</sup>

Hybridity in the pondweeds is then discussed. As hybrids are admittedly difficult to determine and demonstrate, Hagström states the criteria he used in their recognition. These are, briefly: more or less sterility; more or less deformity or abortion in the stamens and pistils, and especially imperfect pollen; occurrence but rarely and that within the known range of both parents; and all characters of the plant reproducing those of one or the other parent, or being intermediate between them.

The systematic enumeration follows, consisting of two subgenera, five sections, 26 subsections, 138 species, and a large number of hybrids. At this point the reader meets a serious difficulty. There is no key of any kind. In order to identify a *Potamogeton*, it is necessary to read every page of this work, and practically memorize them. By elimination it is often possible to go directly to the subsection including a particular plant, but even this is not always possible, for *P. pectinatus* and *P. filiformis* are put in different subsections, while *P. pusillus* and *P. panormitanus* are put in different series. No bibliography of books consulted is included.

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<sup>5</sup> Hagström, *op. cit.* 8.

Under each species, the important synonymy is given. Then comes a description of the gross morphology including the parts usually employed in distinguishing the species. Next follows a description of the internal morphology, especially of the stem and leaves. In most cases the pollen is not described. In a few it is said to be globose and small, or large. No illustrations of the pollen grains are given. It is not stated whether species having large pollen grains show the same number of chromosomes as those with small pollen grains. As a matter of fact no statement of chromosome number is to be found. Hence a student trying to recognize hybrid plants, as does Hagström, by their pollen, would have to investigate for himself not only the few species suspected, but all of the species in the area to determine their characteristics. Illustrations are included for nearly all of the species. They are text figures from line drawings. These show the shape and veining of the leaves fairly well. For a monograph promulgating a classification based largely on stem anatomy, the illustrations of the stem cross-sections are not detailed enough. These represent the stem by its outline, the outline of the lacunae, and areas of cross-hatching to represent the fibro-vascular bundles. A statement of its range finishes each species. In most cases this is based only on specimens examined, so that many citations are given in northern Europe, a small number elsewhere, and in North America very few. For North America the range is often quoted from Morong, or Robinson and Fernald in Gray's New Manual, but occasionally stated only as North America. Several species widely distributed and long recognized as North American plants, are not listed from that continent.

The North American species of *Potamogeton* are recognized by Hagström largely as has been customary. Since it is such a laborious task to find out what he does do with a species, a summary will be given here. Species treated by Hagström as in current manuals or the most recent revisions: *Potamogeton alpinus*, *P. amplifolius*, *P. bupleuroides*, *P. confervoides*, *P. crispus*, *P. dimorphus*, *P. foliosus*, *P. Hillii*, *P. illinoensis*, *P. lucens*, *P. natans*, *P. Oakesianus*, *P. obtusifolius*, *P. perfoliatus*, *P. polygonifolius*, *P. praelongus*, *P. pulcher*, *P. pusillus*, *P. Richardsonii*, *P. Robbinsii*, *P. rutilus*, *P. strictifolius*, *P. Vaseyi*, and *P. zosterifolius*.



*P. americanus*, var. *novaeboracensis* is listed in the index as *P. novaeboracensis*, but the reviewer has been unable to find it in the text. *P. pectinatus* is not listed for North America, except as the var. *zosteraceus*, which is what he calls our *P. latifolius*. *P. interruptus* is called *P. pectinatus*, var. *diffusus*, f. *interruptus*, but is not recorded for North America. *P. acutifolius* is not credited to the United States, but the old specimen from Lancaster is not discussed. He argues that there are no differences but size between var. *niagarensis* and var. *californicus* of *P. foliosus* and that they should be fused. He records *P. filiformis*, f. *luxuriosus* from Riv. St. Mary, Michigan. This seems to be one of the specimens listed by the present writer in *Rhodora* 18: 135. 1916 as var. *borealis*. Hagström maintains *P. filiformis*, var. *occidentalis*, although no new interpretation or new stations are given. On page 134 of the above cited article, the writer discounted the value of this variety. For *P. Friesii* the name *P. mucronatus* Schrader is adopted, as is done by Graebner in the *Pflanzenreich*. *P. panormitanus* is maintained as a species, instead of as a synonym of, or a subdivision of, *P. pusillus*. *P. Aschersonii*, a South American species is here recorded from Cuba, Sable Island, Nova Scotia, and from Newfoundland. For *P. epihydrus* the name *P. Nuttallii* is adopted. He argues that as Rafinesque described his plant as with "foliis . . . submersis subcordatis" this name must be rejected as not applicable. For *P. fluitans* of Europe he adopts the name *P. nodosus*, and makes *P. americanus* a synonym, but without discussion of the characters that have led Morong, Fryer, Taylor, Robinson and Fernald to treat it as a distinct American species. For *P. heterophyllus* he adopts the older Linnaean name *P. gramineus*, as is now done by Graebner and other Europeans, a procedure which has more recently been taken up by Americans, as Fernald, and House.

Hagström describes the following new plants from the United States and Canada.

*P. vaginatus* Turcz., var. *canadensis* Hagstr. n. var. This is the same plant described four months earlier by the present writer as *P. moniliformis* St. John, and later reduced to the synonymy of *P. vaginatus* Turcz.

*P. pectinatus* L., var. *zosteraceus* (Fries) Hagstr. n. comb.

*P. lacunatus* Hagstr. n. sp. This is a segregate of *P. pusillus* and is recorded from Anticosti to Massachusetts.

- P. lacunatus* Hagstr., f. *Novae-Angliae* Hagstr. n. f. A slender form of the preceding.
- P. conjugens* Hagstr. n. sp. This is a segregate of *P. hybridus* or *diversifolius*. It is recorded from New Jersey, Pennsylvania, and San Louis Potosi.
- P. pulcher* Tuckerm., f. *amphibius* Hagstr. n. f. A form without submersed leaves, found in Massachusetts, Rhode Island, and Delaware.
- P. rotundatus* Hagstr. n. sp. This has floating leaves and lanceolate submersed leaves. It is listed from Nebraska, New Mexico, California, and Chihuahua.
- P. cayugensis* (Wieg.) Hagstr. n. comb.
- P. illinoensis* Morong, f. *rosulatus* Hagstr. n. f. This plant from Florida has very short internodes.
- P. illinoensis* Morong, f. *homophyllus* Hagstr. n. f. This lacks floating leaves. It is recorded from Michigan, Texas, and Michoacan.

Reference has been made to Hagström's recognition of hybrid Potamogetons. Between the North American species, he recognizes 25 hybrids, 15 of these being described as new. In all cases where these hybrids have not also received a binomial name, he coins one. Furthermore, under a number of these hybrids he describes and names numerous subdivisions, varieties, and forms. For instance under *P. gramineus*  $\times$  *perfoliatus* he describes 3 varieties and 27 forms, not all of which are American. A study of his description of these 25 hybrids reveals that in most cases he seems to have applied his various tests of hybridity. The pollen or most of it is stated to be imperfect, the pistils are more or less abortive, seldom setting fruit, the general characteristics of external and internal morphology mimic or are intermediate between those of the alleged parents, and the occurrence is stated within the ranges of parents.

Let us examine, however, the treatment of one species, *P. illinoensis* and its hybrids. It is by all American authorities agreed to be a good species, but a very local one, restricted to a part of the Mississippi valley in western Illinois, eastern Iowa, and Minnesota. Hagström corroborates this range, but describes two new forms, as noted in the list above, which extend the range very considerably, as they occur in Michigan, Minnesota, Florida, Texas, and Michoacan in southern Mexico. The reviewer is by no means convinced that these new forms are properly placed under *P. illinoensis*. The *Wheeler 92* from Pine Lake, Michigan, seems more like *P. lucens*. At any rate, a plant without floating leaves from Texas and southern Mexico

does not sound very closely related to *P. illinoensis*. Likewise, judging from the very brief description of f. *rosulatus*, one can be very skeptical of its relationship with the local northern species. But to get back to the hybrids, Hagström describes hybrids of *P. illinoensis* with five other species: *P. amplifolius*, *lucens*, *nodosus*, *perfolianus*, and *gramineus*, as well as one with both *gramineus* and *lucens*. The accompanying map shows the range of *P. illinoensis* and the occurrence of these reputed hybrids, cross-breeds, bastards, or mules as they are called interchangeably.<sup>6</sup> The localities for these hybrids reach from Mystic Pond near Boston, and from New Haven, clear out to Griffin Lake, in the Gold Range Mountains of British Columbia. It should be noted that what is apparently the same plant from Griffin Lake has recently been described as a new species, *P. melhyensis* A. Bennett.<sup>7</sup> The Massachusetts locality is 800 miles, and the British Columbian one, 1000 miles in an air line from the nearest known station of *P. illinoensis*. The description of each of these hybrids reads in a convincing manner. The external and internal morphology show intermediate characters, and the plants are for the most part sterile. The other alleged parent grows in the area or near it, but how was the crossing produced to form the hybrid at such a distance? The two stations in Minnesota are within the known range of *P. illinoensis*, so that these plants might conceivably have had such a hybrid origin. The other eleven localities, it will be seen are in entirely different drainage systems. Those in Connecticut and Massachusetts are within a few miles of, and drain into, the North Atlantic. Those in Vermont, New York, Michigan and Ontario drain through the St. Lawrence River. Griffin Lake, British Columbia is in the Gold Range Mountains, and drains into the Pacific Ocean. Even if a specimen is barren, and the stem has its vascular bundles arranged somewhat differently, it has not previously been thought a necessary conclusion that it is a hybrid. In case a botanist determines a plant as a hybrid, on whatever ground, he certainly

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<sup>6</sup> The reviewer does not wish even to appear to make fun of Hagström's use of English, which is not always idiomatic or correct. It is always intelligible, and all English speaking botanists will appreciate his writing in it. All new descriptions are in the universal botanical Latin.

<sup>7</sup> Proc. and Trans. Bot. Soc. Edinburgh 29: 50-51. 1924.

must bear the burden of the proof, showing at least that the alleged parent species are present. In these alleged cases of bastard plants, Hagström has not presented any proof. He does not discuss under any of these particular hybrids the method of



FIG. 1. Distribution of *Potamogeton illinoensis*, forms, and hybrids.

1. Hachured area: range of *Potamogeton illinoensis*.
2. Circle around dots: Florida: locality for forma *rosulatus*. Localities for forma *homophyllus*: Pine Lake, Michigan; Texas; Michoacan in south-western Mexico.
3. Solid round dots: localities for *P. illinoensis*  $\times$  *lucens*: Mystic Pond, Massachusetts; New Haven, Connecticut.
4. Circle: localities for *P. illinoensis*  $\times$  *perfoliatus*: Queenston, Ontario; Griffin Lake, British Columbia.
5. Triangle: localities for *P. amplifolius*  $\times$  *illinoensis*: Buckingham, Quebec; Cedar Lake, Ontario, Bar Lake, Manistee, Michigan.
6. Dotted area: localities for *P. illinoensis*  $\times$  *nodosus*: Ferrisburg, Vermont; Little Otter Creek, Vermont.
7. Cross: localities for *P. gramineus*  $\times$  *illinoensis*: Wenham, Massachusetts; Green Lake, Chisago Co., Minnesota; without locality, Canada.
8. Square: localities for *P. gramineus*  $\times$  *illinoensis*  $\times$  *lucens*: Glenwood, Minnesota.

pollination. To this disputed point, he makes no real contribution, merely stating that the species in the subgenus *Coleogeton* are pollinated in the water, while those in *Eupotamogeton* are pollinated by the wind. Graebner says that the species with flowers borne at the surface of the water are wind-pollinated,

while those submersed are pollinated beneath the surface of the water. Fryer suggested at one time that insects might cause the pollination of some of the species, but this has never been demonstrated. Assuming, for the sake of the argument, that all of these six species involved are wind-pollinated, would that make the occurrence of hybrids between them any more probable? The great cyclonic storms that sweep across the continent do have a constant direction from west to east. It might be that the strong wind would pick up pollen grains of *P. illinoensis* one day in the Mississippi valley, and the next day deposit them in Connecticut or Massachusetts. Similar cases have been recorded of pine pollen blown hundreds of miles from the nearest known trees. But, will this explanation work both ways? How is the pollen from *P. illinoensis* in say Minnesota to be blown against the prevailing winds, across the great plains, across the Rocky Mountains, across the Selkirk Mountains, to Griffin Lake in the Gold Range Mountains of British Columbia? To the reviewer this seems preposterous.

Yet this whole case is much like the one shown up by Fernald<sup>8</sup> in his review of Forsaith's paper which describes on the basis of imperfect pollen frequent hybrids between *Epilobium angustifolium* and *E. latifolium*. Fernald points out that in their external morphology these plants show no intermediate characters and that the localities of these reputed hybrids often lack one of the alleged parents. He tabulates many where the nearest known locality for the other parent is hundreds of miles away, or even 1000 miles, as from Surrey, England, to Iceland. Needless to say this casts a very serious shadow over the value of using imperfect pollen as a test of hybridity. To be sure Hagström (pp. 11, 54) admits that *P. Robbinsii* has mostly sterile pollen, and rarely fruits, yet he positively maintains it as a good species; writing,

It cannot be a hybrid between any modern species. Might not the sterile pollen and the scanty fruiting possibly suggest a survivor from times climatically more favorable to it than the present one? Might we not here have before us a dying species, now-a-days maintaining itself principally in a vegetative way?

In some of our larger genera, for instance *Rubus*, the presence

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<sup>8</sup>Fernald, M. L. The assumed hybridization of *Epilobium angustifolium* and *E. latifolium*. *Rhodora* 20: 6-10. 1918.

of imperfect pollen is of no value in separating the hybrids from the true species. Brainerd and Peitersen<sup>9</sup> after prolonged study in the field, herbarium, in cultural plots, and by microscopic examination, have separated the blackberries of New England into 12 species and many hybrids. None of the 12 good species have 100 per cent perfect pollen, and the majority of them have anywhere from 60 to 90 per cent imperfect pollen. These cases, with the many others should demonstrate that the production of imperfect pollen, even a very high percentage of it, is no proof that the plant is a hybrid.

An investigation of the literature of genetics will show that the degree of development of a hybrid depends on the nearness of relationship of the parents. A good statement of this varying completeness of growth of hybrid individuals has recently been given by Longley.<sup>10</sup>

Hybrids may have a short life, never developing beyond a few cells. Others may mature into organisms vigorous vegetatively, but unable to produce flowers and fruit. Others are capable of producing spore mother cells, but these fail to become tetrads. Some can carry out the reduction processes in a characteristic hybrid manner. In crosses between closely related species, pollen-formation shows few signs of irregularities, but the pollen shrivels. Finally there are hybrids between species so closely related that practically no incompatibility exists between the sex cells, and they seem as normal as a typical homozygous species. [p. 313.]

There seems no reason to question the sterile state of these alleged hybrids. Every herbarium is full of sterile specimens. That should cause no surprise to any collector who has hunted for fruiting pondweeds. If he happens to come along at the right time of year, if the water level is not abnormal, if no man or animal has partially destroyed the plants, if he can get a boat or raft or can wade out to the required depth, he may find some *Potamogeton* in fruit, and he considers it a lucky day when he does. Hence the reviewer does not feel that barren or unfertilized *Potamogetons* must be hybrids.

Hagström does not mention ever having grown any hybrid plants or producing them artificially under controlled conditions. It would take many years and ample facilities to breed these

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<sup>9</sup> Brainerd, E., & Peiterson, A. K. Blackberries of New England—their classification. Vermont Agr. Exp. Sta. Bull. 217. 1920.

<sup>10</sup> Longley, A. E. Cytological studies in the genus *Crataegus*. Am. Jour. Bot. 11: 295-317. f. 1-8 + pl. 16-18. 1924.

perennial aquatics. To the best of the writer's knowledge, the only man to approach this was the English botanist Alfred Fryer. For many years in submersed pots, in tubs, and in shallow ponds, he grew and observed pondweeds. He did not make an intensive study of hybrids, but a number of them were raised and studied. In his beautifully illustrated book, his life work on *Potamogeton*, Fryer writes,<sup>11</sup>

The hybrids of *Potamogetons* are not like the hybrids of less variable plants; in some instances they may be constant enough to one type, but in others the variation seems to have no bounds. We find suggestions of not two, but many species, and it is impossible to suppose that these resemblances are accidental or uncontrolled by law. When by observation and actual experiment the law that governs the variation of cross-bred forms of this genus is discovered, wholly or in part, we shall probably get a clearer view of one of the modes by which "species" may have originated.

On the other hand, Hagström writes on page 12,

The hybrids must be studied according as Nature produces them. Cultivation and experiments in hybridization may not lead to great results as to the solution of this intricate question. A thorough study of the specimens already exactly known as to their origin is much more profitable for the purpose of a correct identifying of others. Rather soon you will learn in which way the one or the other species makes itself prevalent to its compartner, and to recognize the so-called intermediate properties.

On the same page he writes,

It has been proved that the hybrid *Potamogeton*-forms can abide at the place where they have arisen for long spaces of time, while at last both the parents or either has become extinct and other species have occupied their place. . . . It has happened that in a small river or on a spot very much retrenched four or five different hybrids partly entangled in one another have been met with. For instance in Gudenaa at Kongensbro in Jutland. From there I have, in my own herbarium, *P. gramineus* × *natans*, *crispus* × *praelongus*, *lucens* × *perfoliatus*, *lucens* × *praelongus*, and *lucens* × *nodosus*. *P. nodosus* itself is at present gone out in Jutland.

Such observations and views as these are strongly at variance with those of Fryer, who spent so many years cultivating the *Potamogetons*. Why Hagström argues so strongly against using experimental breeding as the method of solving the hybrid problem is not quite clear. Throughout his monograph he shows in his treatment of hybrids that he interprets them as best he can according to Mendel's Law. If it was by controlled

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<sup>11</sup> Fryer, Alfred, Bennett A., and Evans, A. H. *Potamogetons of the British Isles* 10. 1915.

experiment and recorded observations that Mendel unraveled the hybrid forms of the sweet peas, and if it is upon this well known law that dependence is placed, why does Hagström argue that breeding experiments would be such an unprofitable way to approach the same problem in the pondweeds?

*Potamogeton illinoensis* has been used as a test. Hagström's use of pollen sterility has not given convincing results. His recognition of intermediate characters in the appearance of the supposed hybrid has not served as a trustworthy check. The ranges of the two supposed parents, although clearly stated, do not seem to influence his opinion. He is the first to make extensive use of stem anatomy in identifying the species and hybrids of *Potamogeton*. The reviewer has no preconceived notions of its value. Still, Hagström places more emphasis on stem anatomy than on any other character of the plant. Judging by the dubious taxonomy derived, this new method seems of but doubtful help. It should not be inferred that the reviewer has been blind to a great deal of good material in this monograph, but it is thoroughly intermingled with the questionable. Through complete lack of any key, no short cuts are possible, and only a specialist familiar with the genus can winnow out the good from the bad.

STATE COLLEGE OF WASHINGTON,  
PULLMAN, WASHINGTON

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The author of the foregoing paper has invited the editor to add a biographical note on this Swedish contributor to American botany.

Johan Oskar Hagström, born 21 March 1860, at Bettna, Strängnäs, Södermanland, died 7 June 1922, at Västra Emtervik, Värmland, Sweden. He became a student in Upsala University in 1879, took his examinations for holy orders in 1883, became curate in Lysvik in 1899, was appointed rector in Västra Emtervik in 1910, and rural dean in 1917. That a busy churchman should find time to become so well recognized as a specialist in *Potamogeton* that he was called upon to elaborate this genus for Neuman's *Sveriges Flora* (1901) and for Lindman's *Svensk Fanerogamenflora* (1918) is a matter of interest. In conversations with botanists in Sweden during the past summer, I gathered that Hagström's work in general was well regarded by them. A list of his papers, chiefly on *Potamogeton* and *Ruppia*, may be found in a brief account in *Botaniska Notiser* 1922: 223, from which this notice is mainly compiled.—T. E. H.





# INDEX TO AMERICAN BOTANICAL LITERATURE

## 1925

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A taxonomic study of *Hymenophytum*<sup>1</sup>

ALEXANDER W. EVANS

(WITH NINETEEN TEXT FIGURES)

The genus *Hymenophytum*, as originally defined by Dumortier (under the name "*Hymenophyton*"),<sup>2</sup> included two Australasian species: *H. flabellatum* (Labill.) Dumort., based on *Jungermannia flabellata* Labill., and *H. Hymenophyllum* (Hook.) Dumort., based on *J. Hymenophyllum* Hook. The generic characters emphasized were the following: a bilabiate involucre, a pseudoperianth lobed and toothed at the mouth, and terminal elaters persistent on the valves of the capsule. All three characters apply to the first species but not to the second, which lacks a pseudoperianth completely and develops deciduous elaters only. In 1846, eleven years after Dumortier's work, the authors of the Synopsis Hepaticarum included both species in the genus *Symphyogyna*, proposed in 1836 by Montagne and Nees von Esenbeck. In this genus the absence of a pseudoperianth has always been insisted upon as an important character. On the basis of this feature *S. Hymenophyllum* (Hook.) Mont. & Nees is clearly a member of the genus, but *S. flabellata* (Labill.) Mont., which has a pseudoperianth, ought not to have been referred to it.

In 1861, Gottsche<sup>3</sup> pointed out the impossibility of retaining *S. flabellata* in *Symphyogyna* and proposed the new genus *Umbraculum* for its reception. This genus is obviously a synonym of *Hymenophytum*, although no mention is made of Dumortier's publication. Gottsche showed that his *U. flabellatum* differed from *Symphyogyna* not only in the possession of a pseudo-

<sup>1</sup> Contribution from the Osborn Botanical Laboratory.

<sup>2</sup> Recueil d'Observations sur les Jungermanniacées 15. 1835.

<sup>3</sup> Bot. Zeit. 19: 3. 1861.

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perianth but also in the ventral position of the sexual organs and called attention to the fact that this character had been brought out by La Billardiére in his original description. He showed further that the ventral lobe of the involucre was larger than the dorsal. In a later treatment of his genus<sup>4</sup> he included the following three species: *U. flabellatum* (Labill.) Gottsche; *U. Muellieri* Gottsche, proposed as new on the basis of Australian specimens collected by F. von Müller; and *U. leptopodium* (Hook. f. & Tayl.) Gottsche, based on *Jungermannia leptopoda* Hook. f. & Tayl. of New Zealand.

In 1877, Leitgeb<sup>5</sup> recognized the genus *Umbraculum* and gave a detailed description of *U. flabellatum* with numerous figures. He showed, among many other details, that the midrib of the thallus enclosed a strand of prosenchymatous cells with thickened walls; that the apex of an ultimate branch often lost its meristematic character and became converted into permanent tissue; that dorsal, ventral, and marginal slime papillae were present on the thallus; and that the sexual organs were borne on greatly reduced ventral branches, instead of being actually ventral in position themselves.

In 1881 Colenso<sup>6</sup> described, under the name *Metzgeria* (*Symphyogyna*) *rugulosa*, a New Zealand plant which he compared with *Symphyogyna flabellata*. He stated that the two were essentially alike in their vegetative structure, but that they differed in the position of their sexual organs, these being ventral in his new species and, in apparent ignorance of the work of Gottsche, dorsal in *S. flabellata*. A few years later he spoke of his plant definitely as *S. rugulosa* and proposed the following New Zealand species as new, all being characterized by ventral sexual organs: *S. foetida*, *S. longistipa*, *S. megalolepis*, *S. platycalyptra*, and *S. platystipa*. He thus admitted species with ventral inflorescences into *Symphyogyna* and apparently, perhaps as a result of further study, assigned a similar inflorescence to *S. flabellata*, since he emphasized the close relationship between this species and the others. Stephani has reduced *S. platycalyptra* to synonymy under *H. flabellatum* and *S. platystipa* to synonymy under *S. leptopoda*.<sup>7</sup> The remaining new species,

<sup>4</sup> Ann. Sci. Nat. Bot. V. 1: 180 (footnote). 1864.

<sup>5</sup> Unters. Leberm. 3: 90-102. pl. 7. 1877.

<sup>6</sup> Trans. New Zealand Inst. 13: 368. 1881.

<sup>7</sup> Jour. Linn. Soc. Bot. 29: 276. 1892.

with the exception of *S. megalolepis*, are all represented in the Mitten Herbarium, but the specimens bring out the fact that the differential characters emphasized by Colenso are slight and based on variable features. In the writer's opinion, therefore, these species are all synonyms of *H. flabellatum*, and *S. megalolepis* should probably be placed in the same category.

In 1889<sup>8</sup> Stephani revived the genus *Hymenophytum* but enlarged its scope so that it included not only the genus *Umbraculum* but also the genus *Podomitrium* of Mitten. The latter at that time had a single species, *P. Phyllanthus* (Hook.) Mitt., based on *Jungermannia Phyllanthus* Hook. of Australasia. Stephani's definition of *Hymenophytum* was accepted by Schiffner,<sup>9</sup> who gave *Podomitrium* and *Umbraculum* the rank of sections. In Stephani's opinion they were hardly distinct enough for recognition, even to this slight extent, and he continued to regard them both as simple synonyms of *Hymenophytum*, as shown by his treatment in the Species Hepaticarum.<sup>10</sup> In 1906, however, Goebel<sup>11</sup> made a careful study of *H. flabellatum* and *H. Phyllanthus* (Hook.) Steph. and showed that the differences between them were greater than Stephani implied. He reached the conclusion, in fact, that they were generically distinct. The same conclusion has been reached by Cavers,<sup>12</sup> who definitely accepts both *Umbraculum* and *Podomitrium* as genera, and also by Campbell,<sup>13</sup> who accepts *Podomitrium* and retains for Gottsche's genus the earlier name *Hymenophytum*.

The thallus of *Hymenophytum*, in this restricted sense, is clearly differentiated into a prostrate, terete rhizome, liberally supplied with rhizoids, and an ascending or erect aerial portion without rhizoids (see FIGS. 1-5). In the latter a cylindrical and wingless stipe, representing a continuation of the rhizome, broadens out into a flat, leaf-like expanse, limited in growth and usually several times dichotomous. The successive dichotomies are close together and the branches, in their most typical development, form a flat circular cluster, tending to lie in a

<sup>8</sup> Hedwigia 28: 160. 1889.

<sup>9</sup> Engler-Prantl, Nat. Pflanzenfam. 13: 54. 1893.

<sup>10</sup> Mém. Herb. Boiss. 11: 1. 1900.

<sup>11</sup> Flora 96: 170-182. f. 128-135. 1906.

<sup>12</sup> New Phytol. Reprint 4: 68. 1911.

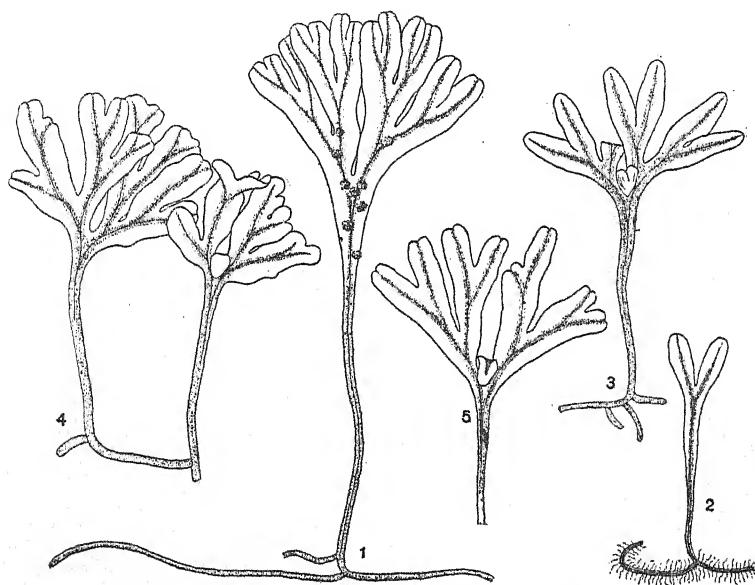
<sup>13</sup> Proc. Nat. Acad. Sci. 1: 36. 1915.

horizontal plane. This condition, however, is frequently not realized, the cluster being often simpler, more cuneate in outline, and lying in the same plane as the stipe. Between these two extremes are all possible intergradations. In the flat portion of the thallus there is a further differentiation into a thickened midrib, with a strand of elongated cells, and broad unistratose wings. The margins of the latter at first bear scattered, two-celled slime papillae, which may leave slight irregularities when they disappear; otherwise the wings are perfectly entire. In cases where the highest development is attained these wings are continuous around the apex, the midrib gradually thinning out and coming to an end. The genus is further characterized by very short sexual branches, growing out from the ventral surface of the midrib and bearing the sexual organs on what is morphologically the dorsal surface. The male branch, as Goebel clearly shows, has undergone extreme reduction. It consists of nothing more than a small, cushion-like protuberance, and it was only by comparing it with the less reduced male branch of *Podomitrium Phyllanthus* that its true nature could be determined. The female branch also is strongly reduced, but less so than the male branch. The earlier writers, as we have seen, described the involucre as bilabiate, with the ventral lip larger than the dorsal. Goebel shows, however, that the ventral lip should be interpreted as the wing of the female branch, continuous around the apex, as it so often is on a vegetative branch. The involucre itself, therefore, is represented simply by the short dorsal lip. Immediately around the archegonia, in case fertilization has taken place, a cylindrical pseudoperianth, toothed at the open mouth, makes its appearance; and within this a massive calyptra, bearing unfertilized archegonia on its surface, surrounds the developing sporophyte. The valves of the mature capsule have band-like thickenings on some of the cell walls.

In Stephani's *Species Hepaticarum* the group "B," which corresponds with *Umbraculum*, contains only two of the three species which Gottsche had assigned to his genus: *H. flabellatum* and *H. leptopodum* (Hook. f. & Tayl.) Steph. His third species, *U. Muelleri*, is listed among the synonyms of *H. flabellatum*. In 1911 Stephani proposed, as a new species, *H. pedicellatum* of Patagonia, based on specimens collected by Skottsberg;

and in 1922 Pearson made another addition to the genus, *H. furcatum*, based on specimens from New Caledonia collected by Compton. These four species are apparently the only ones now assigned to the genus in its restricted sense.

When the characters of these species, as recorded in the literature, are compared they are found to be misleading and unsatisfactory. Take the female branches, for example. In *Umbraculum flabellatum* Gottsche states that the ventral lip



FIGS. 1-5. *HYMENOPHYTUM FLABELLATUM* (Labill.) Dumort.

Thalli: 1, with male branches, from a New Zealand specimen, *Colenso* 2035; 2, sterile, from another New Zealand specimen, *Colenso* 2133; 3, with a female branch, from the type material of *H. pedicellatum*; 4 and 5, with female branches, from Juan Fernandez specimens, *Skottsberg*. All  $\times 2$ .

of the involucre, i. e. the wing of the female branch (if Goebel's interpretation is followed), is entire, while the dorsal lip or involucre proper is laciniate-dentate; in *U. Muelleri* he states that the wing of the female branch is dentate and makes no mention of the involucre; in *U. leptopodium* he describes the male plant only. Stephani, on the other hand, states that the wing of the female branch in *H. flabellatum* is spinose and the involucre deeply lacerate, but that in *H. leptopodium* the wing is entire



and the involucre similar. On the basis of these statements Gottsche's *U. flabellatum* would correspond pretty well with Stephani's *H. leptopodium*, while *U. Muelleri* would agree better with *H. flabellatum*.

The illustrations of *H. flabellatum*, of which several have been published, do not clear up the difficulty. In the original figure of *Jungermannia flabellata* by La Billardiére the wing of the female branch and the involucre are entire or perhaps vaguely sinuate; in the somewhat later figure by Hooker<sup>14</sup> the wing shows an apical indentation but is otherwise entire, and the involucre (so far as shown) seems also to be entire; in Goebel's figure<sup>15</sup> several female branches are shown and the wings vary from entire to very sparingly toothed or emarginate; in Cavers' figure<sup>16</sup> the wings are emarginate but otherwise entire. Stephani's own figure of *H. flabellatum* in his *Icones Hepaticarum*, which has never been published, shows the wing with numerous short blunt teeth and a few sharp spines, while the involucre is represented as irregularly lacerate. His figure of *H. leptopodium* shows a vaguely sinuate wing and an irregularly crenate involucre with a single slender tooth. On the whole his figures agree with his descriptions, but his figure of *H. leptopodium* agrees with most of the earlier figures of *H. flabellatum*.

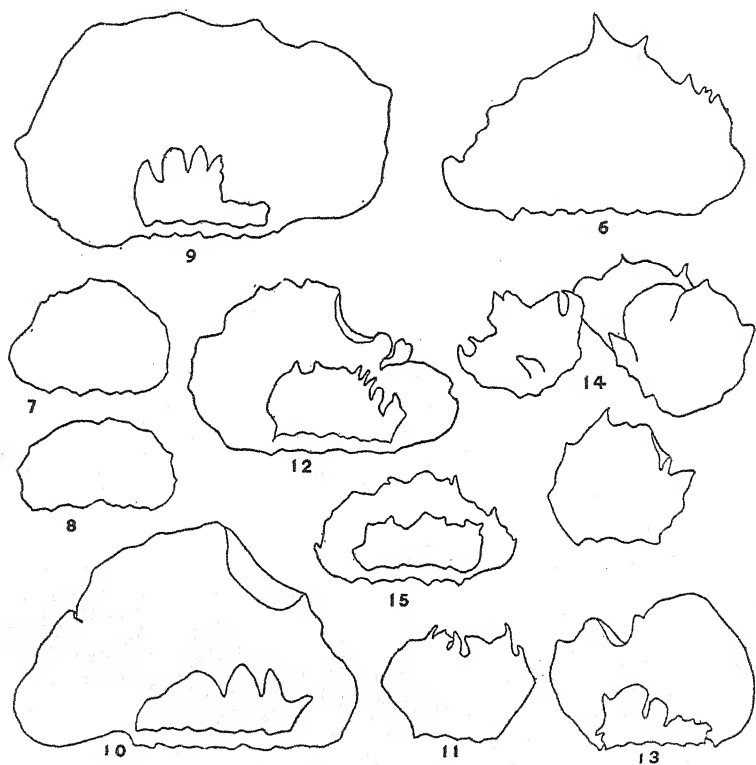
A careful study of the specimens of *Hymenophyllum* in the Mitten Herbarium and other collections shows that the wings of the female branches are exceedingly variable. In FIG. 6, drawn from a specimen of *S. rugulosa*, the wing is much like that in Stephani's drawing, except that the spines are less numerous. In FIGS. 7 and 8, both drawn from a Tasmanian specimen in the Hooker Herbarium, the wings are more nearly entire but show a few minute teeth. In FIG. 9, drawn from a New Zealand specimen labeled *H. leptopodium*, the wing is irregularly sinuate or perhaps vaguely and coarsely crenate. In FIG. 10, drawn from another New Zealand specimen, the wing is scarcely different from the one shown in FIG. 9, but gives a slight indication of a crispate and revolute margin. The involucres in these various specimens were poorly preserved. So far as shown in the figures they are more or less lacerate with rounded to acute

<sup>14</sup> Musc. Exot. pl. 13. 1818.

<sup>15</sup> Flora 96: f. 133. 1906.

<sup>16</sup> New Phytol. Reprint 4: f. 31. 1911.

divisions. When these various figures are compared with one another and with the other figures mentioned above, they clearly indicate that no differential characters can safely be drawn from the sexual branches and involucre in the species under consideration.



FIGS. 6-15. *HYMENOPHYTUM FLABELLATUM* (Labill.) Dumort.

Female branches, sometimes with involucre: 6, from the type material of *Metzgeria rugulosa*; 7 and 8, from a Tasmanian specimen in the Hooker Herbarium; 9, from a New Zealand specimen, *Colenso 2035*; 10, from another New Zealand specimen, *Colenso 1429*; 11, from the type material of *H. pedicellatum*; 12-14, from Juan Fernandez specimens, *Skottsberg*. All  $\times 17$ .

The characters drawn from the vegetative organs are equally unsatisfactory in distinguishing *H. flabellatum* from *H. leptopodium*. In *H. flabellatum*, according to Stephani in the *Species Hepaticarum*, the winged portion of the thallus is repeatedly

dichotomous (up to five times), the forks are close together, and the branch-system formed is suborbicular, owing to the fact that the ultimate branches are all of about the same length. In *H. leptopodium* he states that the branches formed by the first dichotomy are longer than in *H. flabellatum*, and that the branch-system is more irregular. Such differences, however, are not brought out in his unpublished drawings. The branch-system of *H. leptopodium*, as there shown, is essentially the same as that of *H. flabellatum*, and the branches formed by the first dichotomy are not appreciably longer in one species than in the other. The writer's FIG. 1, drawn from a New Zealand specimen labeled *H. leptopodium*, represents a more lax branch-system than those shown in the figures of *H. flabellatum* by Goebel and Cavers; but the differences are without much significance as distinguishing characters, and Stephani himself remarks in connection with *H. flabellatum* that the branch-system is "haud rare multo minor et minus ramosa." In FIG. 2, drawn from a New Zealand plant referred as a variety to *H. leptopodium*, a condition of extreme simplicity is shown.

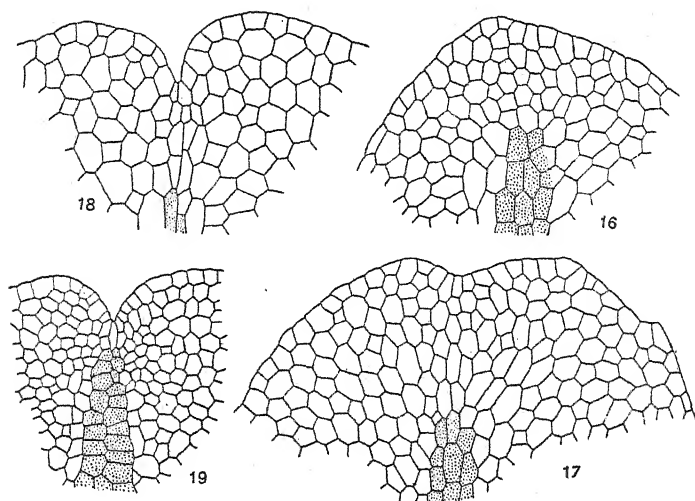
Another difference emphasized by Stephani relates to the ultimate branches. In *H. flabellatum*, according to his account, the midrib comes to an end below the apex, but in *H. leptopodium* it is always excurrent. His unpublished figure of *H. flabellatum*, to be sure, does not support his description, the midribs extending to the extreme tips of the branches in nearly every instance, and the same thing is true of many of the midribs in the figure by Cavers; and yet, if this distinction were actually realized in the plants themselves it would constitute an excellent specific difference. Unfortunately it is not so realized, and in this connection Leitgeb's careful description may be brought to mind. According to his statements the apical portion of an ultimate branch in *H. flabellatum* shows an indentation, as in any growing thallus, but the cells at the bottom of this indentation lose their meristematic character and often acquire brownish walls. When this has happened the growth of the branch has clearly come to an end, and Leitgeb notes that in such cases the midrib ends at some little distance from the apex. The conditions described are brought out by FIG. 17, drawn from a Tasmanian specimen of *H. flabellatum*, and also by FIG. 18, drawn from a New Zealand specimen labeled *H. leptopodium*. Neither figure shows any sign

of an apical cell. In FIG. 17 the apical notch is very shallow, and the cells between it and the end of the midrib are essentially like the neighboring alar cells, except that some of them are elongate in the direction of growth. The condition here represented is shown in its most advanced phase by FIG. 16, drawn from a New Zealand specimen of *H. flabellatum*. Here the apical notch is entirely eliminated, and the cells between the apex and the end of the midrib show no signs whatever of differentiation. In FIG. 18, however, where the notch is deeper, these cells are not only elongate but are also arranged in more definite longitudinal rows. These three figures may be compared with FIG. 19, drawn from another New Zealand plant labeled *H. leptopodum*. In this case the growth of the branch had clearly come to an end, but the apical cell had maintained its integrity and the neighboring cells had not advanced very far beyond a meristematic condition. The figure is somewhat schematic, owing to the fact that the apical cell is shown in optical section, the cells immediately covering it not being indicated. Although the branches of a single branch-system sometimes illustrate only one of the four types shown, it is not unusual for two or three of the types to be present. It is clear, therefore, that differences in the apical portion of the ultimate branches do not yield trustworthy distinctions.

The alar cells, as described by Stephani, average only  $38\mu$  in diameter in *H. flabellatum*, while in *H. leptopodum* they measure  $76 \times 46\mu$ . According to the writer's observations the size of the cells seems to be strongly influenced by environmental conditions, and the cells in plants labeled *H. flabellatum* are often fully as large as in plants labeled *H. leptopodum* and show an equally marked tendency to be longer than broad. No safe distinctions, therefore, can be drawn from differences in the size of the cells. The cells, moreover, are not so uniformly thick-walled as Stephani intimates. In some cases they are thin-walled throughout and, even when thickening is apparent, minute trigones can often be demonstrated.

One other statement made by Stephani in regard to *H. leptopodum* may be alluded to. He says that the branches formed by the first dichotomy are often wingless at the base. His unpublished figure shows wings on these branches throughout their entire extent, these wings being apparently short-decurrent

on the stipe, and FIGS. 1 and 2 represent decurrent wings even more clearly. According to the available material, plants labeled *H. leptopodium* almost always show wings of this character, the decurrent portions narrowing very gradually or more abruptly as the case may be. Sometimes, however, and this is even more true of plants referred to *H. flabellatum*, the wings are not decurrent on the stipe, and the wingless condition may extend for a variable distance above the first dichotomy. The region



FIGS. 16-19. *HYMENOPHYTUM FLABELLATUM* (Labill.) Dumort.

Apices of branches, the slime papillae not shown: 16, from a New Zealand specimen, *Micklejohn 83*; 17, from a Tasmanian specimen in the Hooker Herbarium; 18, from a New Zealand specimen, *Colenso 2062*; 19, from another New Zealand specimen, *Colenso 2035*. All,  $\times 100$ .

at the junction of the two branches, where a slight protuberance is present, is especially likely to be without a wing, and no cases have been observed in which the wingless condition extended to the second dichotomies.

If, as we have perhaps a right to assume, the highly differentiated thallus of *Hymenophyllum* is derived from a prostrate, radiculose thallus, winged throughout the greater part of its extent, the wingless portion represents a more "advanced" condition than the winged portion, and the higher up the wingless portion extends the more advanced the thallus has become.

Goebel has shown that one of the leaf-like branches of a thallus, under conditions of feeble illumination and increased moisture in the air, can be made to continue its growth as a cylindrical and wingless rhizome with numerous rhizoids. In this case there is a marked change from one type of thallus to another. Variations in the environmental conditions clearly affect, in a somewhat similar way, the extent of the marginal wings and produce various types of thallus, the differences between which are far less marked than in the change induced by Goebel. A series of forms may thus result, varying from the most advanced condition, in which the wingless portion extends beyond the first dichotomy, to the most juvenile condition, in which the wings are long-decurrent down the stipe. It is inadvisable, of course, to base specific distinctions on intergrading differences of such a type, and the occasional absence of a wing in the neighborhood of the first dichotomy has little significance from a taxonomic standpoint.

From the evidence brought forward the writer feels justified in regarding *H. leptopodium* as a simple synonym of *H. flabellatum*. Apparently Rodway reached the same conclusion in 1916. In the second volume of his work on Tasmanian Bryophyta he does not include *H. leptopodium* definitely as a species, and yet alludes to the fact that Stephani recognizes it.<sup>17</sup> He describes the margin of the "involucre" in *H. flabellatum* as "entire, obscurely toothed or irregularly spinous," thus combining Stephani's characters of *H. flabellatum* and *H. leptopodium*, but he calls attention to the fact that "the involucre is seldom entire."

When the Species Hepaticarum appeared there was no recorded evidence to show that the range of *Hymenophyllum* extended beyond Australasian regions. Stephani's publication of *H. pedicellatum*, however, extended the known range of the genus into antarctic America. According to his description of the new species, the two branches formed by the first dichotomy are terete, thus implying a wingless condition, and he uses this character to separate *H. pedicellatum* from *H. leptopodium*, the corresponding parts of which he now describes as everywhere winged. It will be remembered that he had formerly described them as sometimes wingless at the base. The type

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<sup>17</sup> Papers & Proc. Roy. Soc. Tasmania 1916: 17. 1916.

specimen of *H. pedicellatum* is in the Natural History Museum at Stockholm and has been kindly sent to the writer for study by Dr. Möller. Some of the thalli, such as the one represented in FIG. 3, show the condition described by Stephani even more clearly than it is shown by any of the Australasian specimens of *H. flabellatum*, but the wingless condition is by no means constant, other thalli showing narrow wings decurrent on the stipe and present everywhere above the first dichotomy. Since this character is so inconstant and since the wing of the female branch, as shown in FIG. 11, presents no distinctive features, it seems advisable to include *H. pedicellatum* also among the synonyms of *H. flabellatum*. At the same time it must be admitted that the plants of *H. pedicellatum* are less robust than those of many Australasian specimens, and that no thallus has been observed in which more than three dichotomies were present.

Apparently *Symphyogyna integerrima* Steph. of Juan Fernandez represents still another synonym. In Stephani's figure a rather poorly developed thallus with only three dichotomies is shown, the wings being decurrent for a short distance down the stipe. According to the descriptions the marginal alar cells measure  $36 \times 18 \mu$ , the submarginal  $27 \times 27 \mu$ , and those near the midrib  $45 \times 27 \mu$ . These relatively small dimensions, even if they were fairly constant, would not have much significance in separating the species from *H. flabellatum*, unless supported by other differential characters of importance, and no such characters are brought out. The sterile type specimen of *S. integerrima*, collected by Skottsberg, is in the herbarium of the University of Upsala, and this too, has been kindly sent for examination. It fully supports the conclusion drawn from Stephani's descriptions and figure and shows, moreover, that the alar cells along the margin are by no means constantly elongate; many of them are isodiametric and essentially like the submarginal cells. In view of the complete sterility of the type it may have been difficult to decide, in the absence of other evidence, whether it belonged to *Hymenophyllum* or to the dendroid group of *Symphyogyna*. Such evidence is supplied by the abundant fertile material of *H. flabellatum*, since collected by Skottsberg in the archipelago of Juan Fernandez, and also by the fact that the ultimate branches of the type

show the characteristic slime papillae along the margin. So far as known, marginal papillae are not present in the dendroid species of *Symphygyna*. The Juan Fernandez material of Skottsberg's later collection is represented in FIGS. 4 and 5, while FIGS. 12-14 show the parts associated with the archegonia. It will be seen that these are essentially like the figures drawn from the Tasmanian and New Zealand specimens. In FIG. 14 the wings of a complex female branch are illustrated; it consisted of several coalescent lobes, almost free from one another down to the base and perhaps representing the union of two or more branches. Such anomalous structures are occasionally present in material from other sources.

In proposing *H. furcatum* as a new species Pearson compared it with *H. flabellatum* but stated that it was a much larger plant, that the thalli had fewer segments, that the branch-system formed was not flabelliform, that the alar cells were larger and that their walls were thin and destitute of trigones. In *H. flabellatum*, according to his account, "the walls are somewhat thick with distinct trigones." His measurements for *H. furcatum* are as follows: stems 2.5-3.8 cm. long; segments 1.25-2 mm. wide; alar cells  $75 \times 50 \mu$ . It will be seen at once that his distinctions are based on variable features. The sterile type material of *H. furcatum* is deposited in the British Museum of Natural History, and the writer has had the privilege of studying two of the thalli. So far as these show, there is nothing definite to distinguish the New Caledonian species from *H. flabellatum*. Some of the New Zealand specimens, in fact, are considerably larger, reaching a length of 6 cm., while others show fewer branches. The wide range of variation in the size of the alar cells of *H. flabellatum* has already been commented upon, and it will be seen that Pearson's measurements agree closely with those given by Stephani for *H. leptopodum*. The absence of trigones, moreover, can not be relied upon as a distinctive feature. Even in typical Australasian material of *H. flabellatum* these structures are by no means constant, and they are never large enough to be conspicuous. It seems necessary, therefore, to consider *H. furcatum* another synonym of *H. flabellatum*.

Two specimens of *H. flabellatum* in the Mitten Herbarium, one collected by Seeman in the Fiji Islands and the other by Weir in Colombia, represent interesting extensions of range.



The Fiji Island specimens are sterile but show marginal slime papillae and agree closely with Australasian material. In one of the thalli studied the branches formed by the first dichotomy were almost wingless; in another the branch-system was winged throughout. The Colombian specimen was given a manuscript name by Mitten, but the writer can find in it no differential characters, and FIG. 15, representing the wing of a female branch, might easily have been drawn from a New Zealand plant.

A full synonymy of the species follows:

HYMENOPHYTUM FLABELLATUM (Labill.) Dumort.

*Jungermannia flabellata* Labill. Nov. Holland. Spec. Pl. 2: 109. pl. 254, f. 1. 1806.

*Hymenophyllum flabellatum* Dumort. Recueil d'Obs. sur les Jung. 25. 1835.

*Jungermannia leptopoda* Hook. f. & Tayl. Jour. Bot. 3: 571. 1844.

*Symphogyna flabellata* Mont.; Dumort d'Urville, Voy. au Pôle Sud 1: 216. 1845.

*Symphogyna leptopoda* Tayl.; G. L. & N. Syn. Hep. 482. 1846.

*Umbraculum flabellatum* Gottsche, Bot. Zeit. 19: 5. 1861.

*Umbraculum Muelleri* Gottsche, Ann. Sci. Nat. Bot. V. 1: 181 (footnote). 1864.

*Umbraculum leptopodum* Gottsche, loc. cit.

*Metsgeria rugulosa* Col. Trans. New Zealand Inst. 13: 368. 1881.

*Symphogyna megalolepis* Col. Trans. New Zealand Inst. 16: 353. 1884.

*Symphogyna foetida* Col. op. cit. 354.

*Symphogyna longistipa* Col. op. cit. 355.

*Symphogyna platycalyptra* Col. Trans. New Zealand Inst. 19: 300. 1887.

*Symphogyna platystipa* Col. Trans. New Zealand Inst. 21: 78. 1888.

*Hymenophyllum leptopodum* Steph. Mém. Herb. Boiss. 11: 5. 1900.

*Hymenophyllum pedicellatum* Steph. Kungl. Svenska Vet.-Akad. Handl. 46<sup>o</sup>: 11. f. 2, a. 1911.

*Symphogyna integerrima* Steph. op. cit. 13. f. 2, e.

*Hymenophyllum furcatum* Pears. Jour. Linn. Soc. Bot. 46: 19. 1922.

The preceding study is based on the examination of a series of specimens in the herbarium of the New York Botanical Garden and the Yale Herbarium, supplemented by a few additional specimens from various other sources. A list of these specimens follows. Those designated "M." are in the Mitten Herbarium belonging to the Garden; those designated "N. Y.," in the general Garden Herbarium; those designated "Y." in the Yale Herbarium or in the private collection of the writer. The stations for the species proposed by Colenso, so far as these have been studied, are taken from the published descriptions; the specimens are simply marked "New Zealand" in the Mitten Herbarium.

AUSTRALIA: Apollo Bay, Müller (M., probably a part of the material upon which *Umbraculum Muelleri* was based); Illawarra, King (M.); Clarendon River, 1882, Rudder (M.).

TASMANIA: without definite localities, Gunn (M., from the Hooker Herbarium); Archer (M.). The type of *Jungermannia flabellata*, which has not been seen by the writer, was collected on the same island.

NEW ZEALAND: without definite localities, Hooker (M., probably a part of the original material of *Jungermannia leptopoda*); Kerr (M.); Joliffe (M.); Craig (Y.); Colenso 537 (M.), 1216 (M.), 1227 (N. Y.), 1284 (N. Y.), 1929 (M.), 2035 (N. Y., Y.), 2062 (N. Y.), 2129 (M.), 2133 (M.), 2153 (N. Y.), 2162 (N. Y.); Otago, Lyall (M.); Point Cooper, Lyall (M.); about four miles south of Norsewood, Waiwapa County, 1880, Colenso (M., type of *Meizgeria rugulosa*); near Mataman, Waiwapa County, 1883, Colenso (M., type of *Symphyogyna foetida*); near Norsewood, 1883, Colenso (M., type of *S. longistipa*); same locality, 1886, Colenso 1429 (N. Y., Y., type of *S. platycalyptra*); Mt. Bruce, Wairarapa, 1913, Gray 41 (Y., from the herbarium of D. Lillie); Lake Wakatipu 1918, Micklejohn 83 (Y., from the same herbarium).

NEW CALEDONIA: Mt. Canala, 1914, Compton 1211 (type of *H. furcatum*).

FJI ISLANDS: without definite localities, Seemann (M.).

JUAN FERNANDEZ: Masafuera, 1908, Skottsberg 43 (Upsala Herbarium, type of *Symphyogyna integerrima*); Skottsberg 47 (Upsala Herbarium, determined by Stephani as "*Symphyogyna*

sp." ); various localities on the same island, 1917, C. & I. Skottsberg.

COLOMBIA: "Andes Bogotenses," Weir (M.).

CHILE: Huafo Island, 1908, Skottsberg 123 (Stockholm Herbarium, type of *H. pedicellatum*).

# Development of prothallium and apogamous embryo in *Pellaea glabella* Mettenius<sup>1</sup>

F. L. PICKETT AND MILDRED E. MANUEL

(WITH THIRTY-TWO FIGURES)

Several years ago attention was called to the clear distinction between *Pellaea atropurpurea* (L.) Link and *Pellaea glabella* Mettenius.<sup>2</sup> At that time cultural studies were undertaken to determine whether or not any distinction could be found between the gametophyte generations of these two closely related forms. Later a brief descriptive note was published, and attention was called to the apogamous nature of *P. glabella*.<sup>3</sup> Within the past two years it has been possible to finish the morphological study, as well as to determine certain adaptive characteristics of this fern.

## DEVELOPMENT OF PROTHALLIUM

In August, 1923, fronds of *P. glabella* were collected on the limestone cliffs in Monroe County, Indiana. Spores from these fronds were used in starting cultures on Knop's solution and on soil taken from the same place as the fronds. Prothallia grew vigorously, and as far as could be determined, normally, on the soil. Rather striking variations, noted below, occurred in the water cultures.

The spores of *P. glabella* are dark brown in color, obscurely tetrahedral in shape, and show numerous, low, rounded, irregular ridges. This dark exospore is hard and brittle, breaking irregularly when the spores germinate. Sowed on one-half strength Knop's solution at room temperature, the spores show a large percentage of germination in ten days. The swelling spore bursts the exospore, protrudes through the opening and shows many oil globules. Within a day chloroplasts begin to appear.

The prothallial plate may be formed by successive divisions of the second cell formed, or it may result from repeated divisions

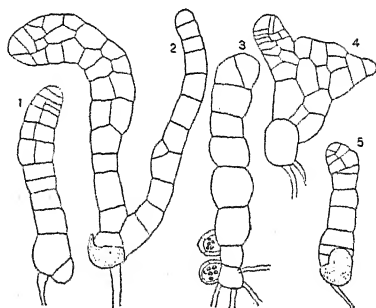
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<sup>1</sup> Contribution No. 3 from the Department of Botany of the State College of Washington.

<sup>2</sup> Pickett, F. L. A peculiar form of *Pellaea atropurpurea* Link. Am. Fern Jour. 4: 97-101. 1914.

<sup>3</sup> Pickett, F. L. Is *Pellaea glabella* Mett. a distinct species? Am. Fern Jour. 7: 3-5. 1917.

of the tip cell of a protonema-like chain of 2-20 cells (FIGS. 4 and 1, 2, 3, 5). It does not grow regularly and symmetrically. It shows no clearly distinguishable apical cell, but rather a group of cells equally active. Plants grown on the culture solution show a tendency to produce chains of cells or ribbon-like structures, 2-5 cells wide and three to four times as long, with the individual cells markedly elongated, before a differentiated meristematic group appears. Grown on soil the plate formation appears earlier and is quite evident within two months from the sowing of the spores. For a time they have a somewhat cordate form but become very unsymmetrical with irregular margins as they grow older. As shown in FIGS. 6-10 some striking forms are found. Even branched forms as shown in FIGS.



FIGS. 1-5 show young sporelings with characteristic forms; FIG. 4 from a soil culture and 1, 2, 3, and 5 from water cultures,  $\times 50$ .

2 and 11-15, are not rare in some cultures. Rhizoids are produced freely by the cells first formed, and on the vertical prothallia of crowded cultures they are produced on either or both surfaces.

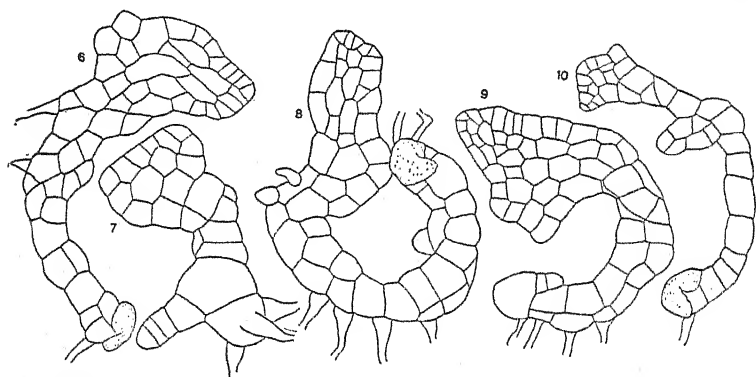
Among the hundreds of specimens examined closely, not one plant has been found showing indication of archegonial growth. Antheridia, on the other hand, are fairly common. In crowded cultures they seem especially abundant, growing upon dwarfed vertical forms and upon larger more fully expanded forms. FIG. 3 shows an extreme case of two antheridia on a very small, filamentous form. A few plants examined seem to have antheridia and at the same time well-developed apogamous embryos, although not enough of such have been found for the careful examination necessary to make this sure. The antheridia

found are normal in development and function. Repeatedly, specimens have been observed discharging living, swimming sperms.

#### DEVELOPMENT OF APOGAMOUS EMBRYOS

The development of apogamous embryos in ferns has been described quite fully in recent years. The fact that such development has not been described for *P. glabella*, together with the occurrence of unique features in the case of this fern, seems sufficient reason for a detailed account at this time.

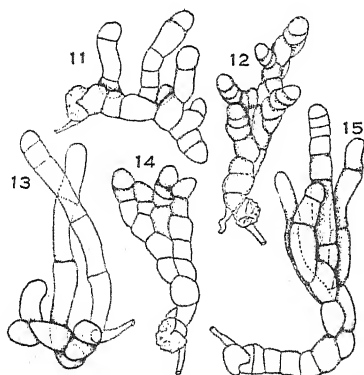
About three months after the germination of spores on soil, the first embryos appear on prothallia about 1.2 mm. wide and somewhat longer. The first indication of embryo develop-



FIGS. 6-10 show various types of development up to plate formation. FIG. 7,  $\times 85$ ; others  $\times 50$ .

ment is the appearance of a small, slightly darkened area (FIG. 16) usually just behind and continuous with the meristematic mass at the base of the sinus. As shown in sections cut lengthwise of a prothallium and perpendicular to its surfaces, such an embryo is composed of a group of small, active, meristematic cells, continuous with the meristematic mass of the sinus, and extending entirely through the prothallium (FIGS. 17, 18, 19). The cells of these masses are smaller, in general, than those of the mature portions of the prothallium and are actively growing cells as indicated by their small size, new walls, slightly denser cytoplasm, and dividing nuclei. In no case, however, does it seem probable that the active tissue has developed from a single initial cell. Appearance bears out the suggestion

that the mass has arisen through renewed activity of otherwise normal prothallial cells. This idea is further strengthened by the fact that later growth of the embryonic mass is brought about, not only through the division of the first differentiated cells, but through an extension of activity involving a rejuvenation of contiguous prothallial cells as well (FIGS. 19, 20). In no case has evidence appeared showing even the slightest crushing or other injury of prothallial tissue by the growing embryo. It is impossible to say with certainty of marginal cells of the embryo that they belong to embryo or prothallium. This differentiation is carried so far that the first epidermis of the embryo is formed by the changed surface cells of the pro-



FIGS. 11-15. Various branched forms of sporelings,  $\times 30$ .

thallium. Even more striking are the cases, occasionally found, where surface prothallial cells have become changed into trachea-like structures as in FIG. 30.

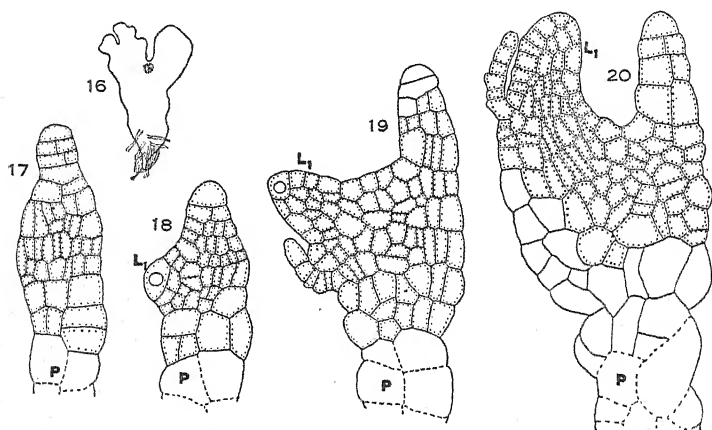
Size rather than age seems to determine the appearance of embryos, inasmuch as marked uniformity in size was evident with prothallia showing the first indications of embryo development.

Growth of the embryo is shown both by a lateral spread of meristematic tissue and by a marked thickening of the mass. The thickening soon becomes evident as a definite hump or projection, usually on the ventral side of the prothallium. It soon becomes more evident through the growth about it of numerous multicellular, transparent hairs (FIGS. 25, 26).

In most cases a leaf is the first distinct sporophytic structure

produced. This grows from the sporophytic mass, usually on the ventral side, but sometimes on the dorsal side of the prothallium, as a cylindrical process, at first pointed (FIG. 26) but later bearing a flattened terminal body (FIG. 21) resembling closely the orbicular or reniform juvenile sporophyte leaves of this fern. The second true leaf may appear on the same side of the prothallium as the first, or, as is not unusual, it may appear on the opposite surface, as shown in FIGS. 22, 23.

In approximately 25 per cent of the plants this leaf is preceded by a horn-like process growing from the anterior portion



FIGS. 16-20. The beginnings of apogamous embryos. FIG. 16. The first suggestion of embryo formation. FIGS. 17-20. Vertical longitudinal sections through very young embryos; stippled areas show active tissue. All  $\times 140$ . L, leaf; P, prothallium.

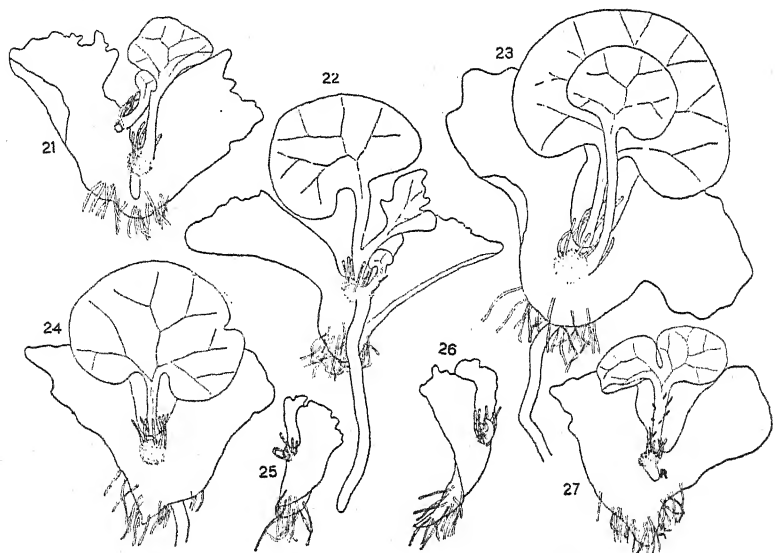
of the embryonic tissue and extending into the sinus, as described and figured by Miss Hayes for *P. atropurpurea*.<sup>4</sup> Such projections are somewhat flattened, more densely chlorophyllous than the prothallial tissue, and usually develop scalariform vessels in their median or basal region (FIGS. 29, 30).

The primary root is usually the second distinct structure to appear, and it is in every way similar to primary roots of normal embryos. Other leaves and roots are produced without any definite order of succession, although the young sporophytes in general have more leaves than roots.

<sup>4</sup> Hayes, D. W. Some studies of apogamy in *Pellaea atropurpurea* (L.) Link. Trans. Am. Micro. Soc. 53: 119-135. 1924.



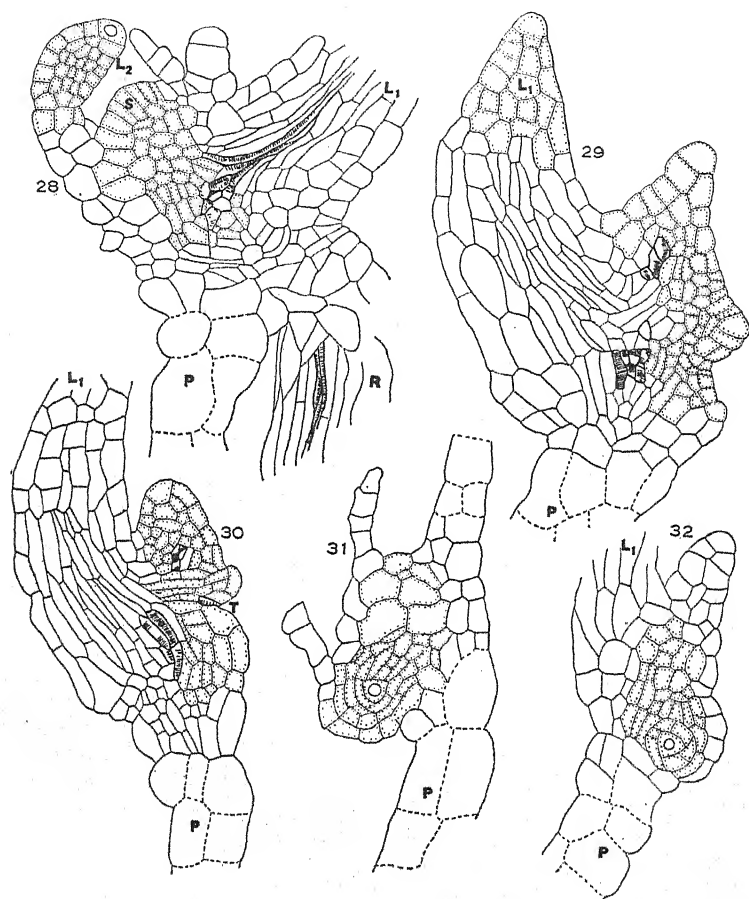
The horn-like structure mentioned above is a direct outgrowth of the meristematic tissue at the base or on the side of the sinus, whereas the first leaf develops from the embryonic tissue behind the sinus (FIGS 29, 30). Soon after the embryonic tissue becomes evident, sections show a clearly differentiated superficial apical cell, through the divisions of which the leaf is formed. This cell is superficial to embryo and to the prothal-



FIGS. 21-27. Apogamous sporophytes. FIG. 21 shows two well developed embryos on one prothallium. FIG. 22 shows the first leaf from the dorsal surface and the second leaf from the ventral surface of the prothallium. FIG. 23 shows root and first leaf from the ventral surface, but the second leaf from the dorsal surface. FIG. 24 shows both leaf and root from ventral surface. FIG. 26 shows an early stage in the development of the leaf. FIG. 27 shows a leaf on the ventral surface, and the beginning of a root, R, on the dorsal surface.  $\times 8$ .

lium as well. As already mentioned, vascular elements appear in the rudimentary leaf sometimes seen. In such cases these vessels are the first vascular elements to be differentiated. In other cases the first differentiated tissue is found near the base of the first true leaf. From this point, by the differentiation of other new tissue, the vascular elements appear in the leaf, and make connection with the later formed elements of stem and root.

The first root is formed through the activities of a typical tetrahedral cell formed some distance in the embryo from the



FIGS. 28-32. Sections of young embryos. FIG. 28. Showing beginning of stem, after two leaves and root are well started. Vascular elements are well developed in root and first leaf. FIG. 29. The differentiation of tissue behind a leaf tip, and two distinct tracheal groups. FIG. 30. A surface cell, T, has developed thickened walls typical of tracheae. FIGS. 31 and 32 show the well marked apical cell of root. All  $\times 140$ . L<sub>1</sub>, L<sub>2</sub>, first and second leaf; P, prothallial cells; R, root; S, stem.

base of the first leaf (FIG. 32). As is usual in normal fern embryos, this cell is large and very prominent. It first appears as a dis-

tinct cell surrounded by the undifferentiated tissue mass of the embryo. Through its division a distinct root cap and vascular tissues are formed before the root tip emerges from the embryonic mass (FIG. 31). A second root is formed later, beginning with the appearance of a distinct cell in the primary meristematic mass of the embryo, and developing, as just described for the first. Later development of these roots is in every respect similar to that in normal embryos. For a time differentiation of tissues extends in both directions from the first scalariform vessels formed a little way behind the root tip, until the vascular tissues of leaf, stem, and root are united.

The stem develops some time after the leaf and root are well started. No clearly marked apical cell is present; but an active meristematic tissue mass, including a large part of the central area of the embryo, extends to a quarter near the first true leaf, and soon differentiates into stem tissues (FIG. 28). The differentiation of this comparatively large mass of tissues makes readily possible the complete union of vascular elements of root, leaf and stem mentioned above.

The growth and activity of a prothallium continues for several weeks after the appearance of an embryo. Even when the sporophyte shows two well developed leaves the prothallium may appear normally green and active. Several prothallia have been examined showing the beginning of more than one embryo, and a few examples of two well developed embryos on one prothallium have been noted (FIG. 21). Where more than one embryo is formed, those appearing later form near the margins adjacent to the sides of the sinus.

#### SUMMARY

The prothallia of *Pellaea glabella* have a normal development from the spore, and show the usual reactions to growth conditions.

The prothallia sometimes produce normal antheridia and sperms, but no archegonia, so sporophytes are produced apogamously only.

Apogamous embryos arise through the activity of cell masses involving comparatively mature tissue of the prothallia.

PULLMAN, WASHINGTON

## On the number of chloroplasts in the cells of the sporophyte of *Anthoceros laevis*

ATHA A. PINNICK

In a study of the morphology of the gametophyte and sporophyte of *Anthoceros laevis* L., the writer was somewhat surprised to find in stained microtome sections of the sporophyte the presence of but one chloroplast in each cell, since in the literature one is given the impression that sporophyte cells contain regularly two chloroplasts (Campbell '18, pp. 121, 142, 597). Inasmuch as the single chloroplast in each cell of the gametophyte, in all North American species, seems to be an organ as permanent as the nucleus, it would be natural to suppose that the cells of the sporophyte might contain two chloroplasts, one being derived from the egg and the other from the sperm in the form of a very small primordium.

Hofmeister, as early as 1862, stated in regard to the number of chloroplasts found in the sporophyte that cells of the upper part of the young fruit [*A. laevis* L. and *A. punctatus* L.] contain without exception *two* chlorophyll bodies; but that in the inner tissue of the stem [gametophyte] the appearance of two chlorophyll bodies is unusual.

Campbell ('18, p. 142) in describing the sporophyte of *A. fusiformis* and *A. Pearsoni*, says that there is a doubling of chloroplasts in the sporophyte, and specifically that "each epidermal cell contains two large chloroplasts like that of the gametophyte." He refers also to Schimper ('85) as having noted that the chloroplasts double in the sporophyte of *Anthoceros*. The statement of Schimper (*loc. cit.* p. 21) pertains to *A. laevis*.

The spore-mother-cell shows regularly only one chloroplast. Therefore the presence of two chloroplasts in the vegetative cells of the sporophyte would be strange and not easily explained. Strasburger ('80) and Davis ('99) have traced the complete history of the spore-mother-cell and its two divisions to form the tetrad. Barring nuclear details, it is not at all difficult to observe all phases of the division of the spore-mother-cells in the fresh material, since the spores mature gradually and the spore-mother-cells readily separate from each other.

In a large spore-mother-cell the chloroplast is very conspicuous, and is seen as a thickened mass in one side of the cell. This large chloroplast is yellowish green in color and contains starch and other granules, which become more numerous and prominent with further development. The chloroplast finally elongates and resembles a thick crescent curved about the nucleus. As the chloroplast divides the two equal portions move apart but are connected by cytoplasmic filaments.

The spore-mother-cell now elongates and the second division of the chloroplast is identical with the first. According to Davis ('99) both chloroplasts may be active at the same time or one may be in a more advanced state of fission than the other. The cell finally appears broader, in proportion to the length, and when the four chloroplasts are formed they are grouped in an orderly arrangement about the centrally placed nucleus. These chloroplasts are all formed before nuclear division occurs in the spore-mother-cell. After final nuclear division one nucleus remains in contact with each chloroplast.

*A. laevis* and *A. punctatus* are the only two species common in the vicinity of Indiana University. All observations mentioned pertain to the former species.

Comparisons were made between chloroplasts of the gametophyte and of the sporophyte. Each cell of the gametophyte shows one very large chloroplast with the characteristic pyrenoid in the center. This chloroplast is granular and somewhat globular, while the contents differentiate prominently with stains. Hofmeister ('62) has described the chloroplasts in elongated cells of older shoots as being flattened and sometimes spindle-shaped, while they also appear flattened in the epidermis. Observations seem to verify these conclusions. Hofmeister ('62, p. 7) also found that the chloroplasts in the interior of the sporophyte are smaller than those in the sporophyte epidermis. Campbell ('18), however, seems to imply that epidermal chloroplasts are as large as in any other cell, for he compares the two large chloroplasts of the epidermis with those of the gametophyte in *A. fusiformis* and *A. Pearsoni*.

McAllister ('14) in his study of structure of the pyrenoid of *Anthoceros* finds that the sporophyte chloroplasts do not differ from those of the gametophyte, although they average considerably smaller. The writer verified this conclusion;

moreover, the smaller chloroplasts of the gametophyte can in no way be distinguished from the larger ones of the sporophyte. McAllister also agrees that each archesporium cell of *A. laevis* contains a minute chloroplast which is difficult to distinguish from granular cytoplasmic cell contents.

The cells at the base of the sporophyte, adjacent to the cells of the gametophyte, show regularly one large chloroplast identical with that of the gametophyte.

While examining preserved material the writer became interested in the number of chloroplasts found in the sporophyte, since the preparations showed only one chloroplast to each cell. After careful examination material was found which showed a very short section of sporophyte cells, where two chloroplasts seemed visible in each cell; but all surrounding cells in the same section had only one chloroplast in each cell. Fresh material was then collected and with free hand sections observations were continued with the result that occasionally two chloroplasts seemed to be visible in certain rows of cells. However, the majority of cells in the same section showed only one chloroplast to the cell.

It seemed reasonable to question whether certain parts of the sporophyte might contain two chloroplasts to a cell while other parts would contain only one. Since the stained microtome sections, in a great number of preparations, showed almost without exception only one chloroplast to the cell in the sporophyte, this conclusion was drawn: that probably the free hand sections of fresh material had the walls and layers of cells so obscured that contents of a single cell would be difficult to determine exactly. As some of the oblique walls are very delicate, and do not show in fresh material clearly, one cannot rely upon free hand sections to give positive results. Fresh material was treated with two per cent. osmic acid and mounted in dilute glycerine. The results showed that if two chloroplasts were occasionally found it was the exception rather than the rule. All stages of young and mature sporophytes, were examined in fixed and stained sections, and the above conclusion was confirmed.

The writer is convinced after obtaining the above results, that only one chloroplast is present in the cells of the sporophyte of *A. laevis*. Therefore it may be possible that sources of error

due to methods of observation are responsible for the report of the presence of the double chloroplast in the sporophyte of *Anthoceros* as published by Campbell ('18) and Hofmeister ('62).

One might explain the presence of an occasional double chloroplast by assuming that after the chloroplast divided the cells failed to divide. It seemed strange, on the one hand, to expect two chloroplasts regularly in the vegetative cells of the sporophyte when only one is found in the spore-mother-cell. But, on the other hand, the sporophyte is formed by the union of two cells or gametes: it therefore would seem that the sporophyte should have two chloroplasts, if the sperm furnishes one or its primordium and the egg the other. However, the egg does not have a fully developed chloroplast, but one merely in the rudimentary stage. Now it is possible that a primordium may be carried by the sperm, but so far as the writer has been able to ascertain, no statement to that effect occurs in the literature.

Again if we make a comparison with *Spirogyra*, we find that one set of chloroplasts in this plant degenerates, just as we find three nuclei in the germinating zygote disintegrating and only one functioning. Now the nucleus is a permanent organ of a *Spirogyra* cell, yet three nuclei completely disintegrate and disappear. For the same reason we may logically assume that the chloroplast is as permanent in *Anthoceros* as is the nucleus. Therefore, if one chloroplast of *Anthoceros* disintegrates, leaving only one to a cell in the sporophyte, that does not disprove the theory that the chloroplast is as permanent as the nucleus.

INDIANA UNIVERSITY

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# INDEX TO AMERICAN BOTANICAL LITERATURE

1922-1925

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